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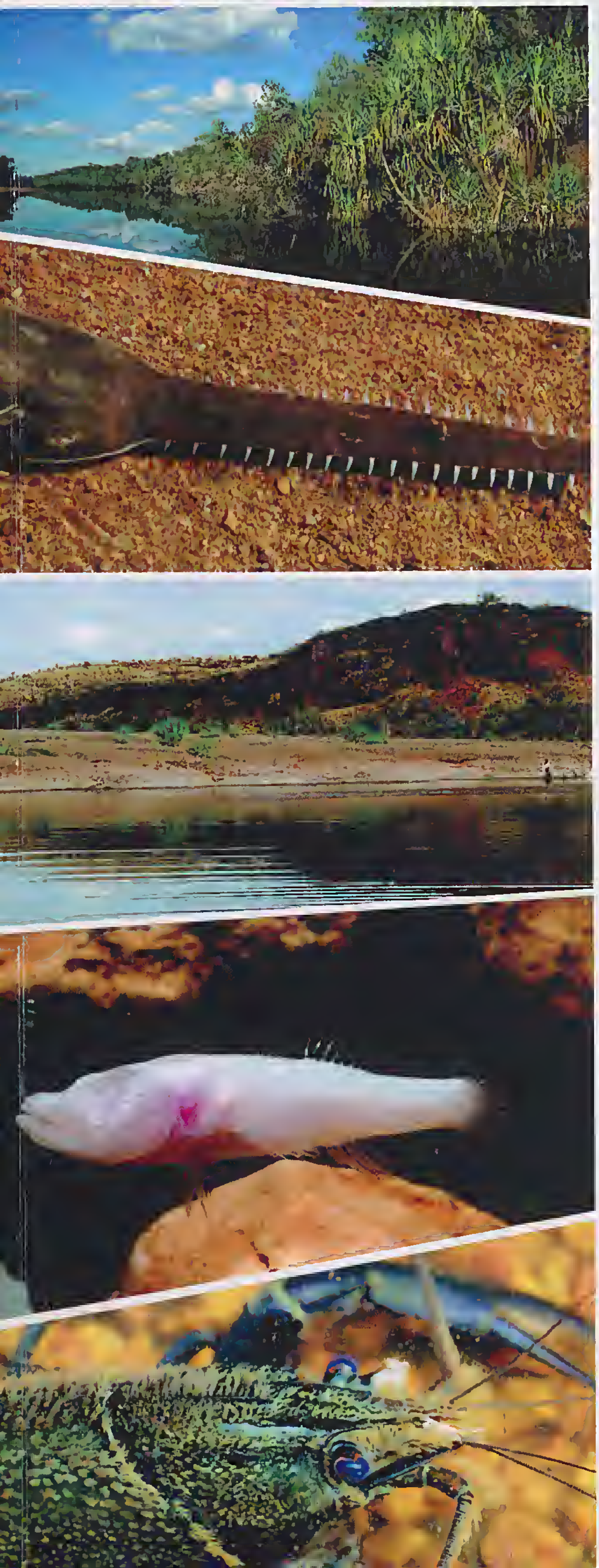

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Inaugural Western Australian Freshwater Fish Symposium

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The Royal Society of Western Australia was founded in 1914. The Society promotes exchange among scientists from all fields in Western Australia through the publication of a journal, monthly meetings where interesting talks are presented by local or visiting scientists, and occasional symposia or excursions on topics of current importance. Members and guests are encouraged to attend meetings on the third Monday of every month (March–November) at 7 pm, Kings Park Board offices, Kings Park, West Perth, WA 6005, or as advertised, in the RSWA Proceedings, Diary of Events.

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The Journal of the Royal Society of Western Australia was first published in 1915. Its circulation exceeds 650 copies. Nearly 100 of these are distributed to institutions or societies elsewhere in Australia. A further 300 copies circulate to more than 40 countries. The Society also has over 350 personal members, most of whom are scientists working in Western Australia. The Journal is indexed and abstracted internationally.

Cover design: The images portray the diversity of inland aquatic habitats and resident fauna of Western Australia embraced in this special issue of the Journal of the Royal Society of Western Australia. Counter-clockwise from the top they are: the Fitzroy River in the Kimberley region; the threatened freshwater sawfish (*Pristis pristis*); the Fortescue River in the Pilbara region; blind cave gudgeon (*Milyeringa veritas*); the critically endangered hairy marron (*Cherax tenuimanus*); Balston's pygmy perch (*Nannatherina balstoni*); and an aerial view of a pool on the Kent River in the State's south-west. Photographs by David Morgan, Mark Allen, Stephen Beatty and Simon Visser.

MUSEUM VICTORIA
15 DEC 2015

Inaugural Western Australian Freshwater Fish Symposium

This volume is dedicated
to the memory of Jon Murphy

AUSTRALIAN SOCIETY for FISH BIOLOGY

Murdoch UNIVERSITY

Freshwater Fish Group &
Fish Health Unit

Centre for Fish & Fisheries Research

Government of **Western Australia**
Department of **Fisheries**

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PREFACE

Inaugural Western Australian Freshwater Fish Symposium

In November 2013, the Inaugural Western Australian Freshwater Fish Symposium was held at the Naturaliste Marine Discovery Centre, Hillarys Boat Harbour, Western Australia. It had been conceived and developed as a forum to assist in the conservation and management of the unique, but relatively little documented, fish and crayfish faunas in the inland aquatic systems of Western Australia. The symposium was attended by over 100 delegates, mostly from Western Australia, but also included attendees from most other Australian States. Twenty-eight speakers gave formal presentations on topics including threatened species, invasive species, fish parasites, sampling techniques, genetics, morphology, new species discoveries, and the management of fishes and their habitats.

The current Special Issue contains 11 papers that detail significant research achievements and management issues relating to Western Australia's unique freshwater fish and crayfish fauna. It is timely, in that much of the fauna is immediately threatened by a decline in surface water quality and availability, the impacts of invasive fishes, habitat degradation and the changing climate, among other factors. The first paper in the issue by Morgan *et al.* presents a much needed overview of fishes in freshwaters of Western Australia including a historical account of taxonomic, ecological and biodiversity discoveries. It represents an important review of the current knowledge of the biodiversity of fishes in each of the ichthyological provinces of Western Australia, specifically the Kimberley Province, Northern Province, Pilbara Province, Southwestern Province and the arid interior Paleo Province, which together constitute half of Australia's icthyological divisions.

The Symposium Keynote Speakers were Drs Adam Kerezsy and Brendan Ebner. The paper by Kerezsy provides an excellent template for Western Australian researchers and managers on the importance of science communication beyond the scientific community. Lessons from the Kerezsy contribution include the example of the conservation of a small endangered fish species which has a relevance extending to organisms other than fish. Ebner *et al.* provide a history of the emergence of underwater video for studying the ecology of fishes and crayfishes in the Australian environment. Some of this work has Western Australian origins, and the review brings together experiences of researchers from across Australia that may assist those researchers and managers that are planning on or currently using this technology in inland aquatic ecosystems.

Duffy *et al.* provide a timely review of the Critically Endangered Margaret River Marron, a species that, without management intervention, may not persist in natural ecosystems beyond the next few decades, as a consequence of the introduction of the more widespread Smooth Marron. Another species that is threatened by introduced species and loss of habitat is Balston's Pygmy Perch, and Morgan and co-authors provide details on the range reduction of this endemic threatened fish. Enhancing fish migration in streams through the construction of fishways is only a decade old in Western Australia, and Beatty and colleagues detail the importance of understanding life-history and swimming ability of target species in the planning, design and construction of fishways in Western Australia. This is a timely publication in light of future predictions of reduced flow in Southwestern Province streams. Hourston *et al.* provide a disturbing finding from a large dataset on fishes in Swan Coastal Plain wetlands, demonstrating that of those wetlands containing fishes, only 12% were found to contain only native fishes, while 42% only supported introduced fishes. Rashnavadi and co-authors examine the flexibility in life history traits of a fish typically of estuarine origin that has penetrated inland into river systems that are impacted by secondary salinisation.

The remaining papers deal with studies in the Kimberley region of the State, a region which offers the highest number of species that are targeted for food, and also the highest diversity of inland fishes in the state. Close *et al.* identified that areas of relatively easy accessibility are most affected by fishing pressure, in contrast to remote regions. Thorburn *et al.* utilised dietary and stable isotope analyses to determine seasonal predator and prey relationships in the Fitzroy River, while Storey and Creagh address the applicability of the Functional Habitat Concept to fishes occurring in the various habitats of the Lower Ord River.

The overwhelmingly positive feedback received from the delegates to the Symposium who were surveyed will ensure that it becomes a reoccurring event. The publication of this Special Issue would not have been possible without considerable support from the Australian Society for Fish Biology, the Department of Fisheries and Murdoch University's Freshwater Fish Group & Fish Health Unit. We are delighted, that in the Centenary year of the Royal Society of Western Australia, the Society has supported the publication of this special issue, which presents an important positive step in conserving our uniquely Western Australian freshwater fish fauna.

David Morgan, Stephen Beatty, Michael Snow & Debra Thomas
Organising Committee, Inaugural Western Australian Freshwater Fish Symposium

REVIEWERS

We would like to extend our gratitude to the reviewers of the various manuscripts within this special issue:

Mark Allen, Patrick Armstrong, Stephen Beatty, Leah Beesley, Michael Calver, Paul Close, Rodney Duffy, Brendan Ebner, Michael Hammer, Pierre Horwitz, Matthew Hourston, Adam Kerezsy, Jason Ledger, Jess Leyland, Michael Lowry, Alan Lymbery, David Morgan, Brad Pusey, Tom Ryan, Michael Snow, Tim Storer, Andrew Storey and Dean Thorburn.

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An overview of the 'freshwater fishes' of Western Australia

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Western Australia's non-tidal waters provide refuges to many unique fishes. Here we provide an overview to synthesise contemporary knowledge on these species with the aim of providing readers with an understanding of their biological, ecological and conservation significance. Western Australian inland aquatic ecosystems provide critical habitats for many obligate freshwater fishes as well as diadromous species that rely on fresh water to complete their life-cycle. Five of Australia's 10 ichthyological provinces are found within the State, three in their entirety. Notable species from evolutionary and biogeographic perspectives include the enigmatic Gondwanan relic *Lepidogalaxias salamandroides* (Salamanderfish) and the ancient jawless fish, the anadromous *Geotria australis* (Pouched Lamprey) in the Southwestern Province. The Pilbara Province supports Australia's only known obligate vertebrate stygofauna, including one of the world's largest stygofauna species, *Ophisternon candidum* (Blind Cave Eel), and two blind eleotrids (*Milyeringa* spp.). The freshwaters of the Kimberley region support three elasmobranchs including *Pristis pristis* (Largetooth or Freshwater Sawfish) and features high species richness and endemicity in the Terapontidae and Eleotridae. The Paleo Province encompasses much of the arid interior of the State, and has very few records of fishes. Western Australian rivers also provide habitat for a small number of euryhaline elasmobranchs that have become vulnerable to extinction elsewhere, and other fishes that utilise these habitats as nurseries. The State supports many fishes that are nationally and internationally listed as threatened or of conservation concern and an increasing number of alien fishes. We collated a total of 102 native fish species that are found within fresh waters of the State, of which 66 are obligate freshwater fish species, three are stygofauna, and a further two have amphidromous and potamodromous populations. In addition, several estuarine species are able to breed in fresh waters, the remainder being diadromous or 'wanderers' that are freshwater vagrants.

KEYWORDS: Kimberley, Pilbara, Southwestern, Paleo, Province, alien fish, endangered fish, endemic

INTRODUCTION

Covering nearly one-third of the Australian continent, Western Australia comprises 5 of Australia's 10 ichthyological provinces (Figure 1). The Southwestern, Pilbara, and Kimberley provinces are all wholly contained within Western Australia, whereas the western edge of the Northern Province and the western portion of the Paleo Province also occur in Western Australia (Unmack 2013). A broad variety of climatic regimes prevail in the provinces, including the temperate Mediterranean climate of the southwest, the sub-tropical and semi-arid climate of the Pilbara and southern Kimberley, the tropical northern Kimberley, and the arid Paleo Province. These climatic templates have undoubtedly influenced the evolution of many unique assemblages and species of fishes in the inland waters of the State.

Scientific contributions to our knowledge of Western Australia's fish fauna began largely during the middle of the last century, with many new species discovered and subsequently described from the 1940s (e.g. Whitley 1944, 1945), 1950s (Shipway 1953), 1960s (Mees 1961, 1962, 1963), and through the 1970s and 1980s (Allen 1975, 1978, 1982, 1989; Hutchins 1977, 1981; Vari 1978; Vari & Hutchins 1978; Ivantsoff *et al.* 1987). Numerous taxonomic, ecological and biogeographical studies followed these earlier works including those on the ecology, behaviour and physiology of the enigmatic *Lepidogalaxias salamandroides* (Salamanderfish) by McDowall & Pusey (1983), Allen & Berra (1989), Berra & Allen (1989, 1991), Pusey (1989, 1990), Pusey & Stewart (1989), Gill & Morgan (1999) and Morgan *et al.* (2000). A series of ecological descriptions of species and habitat associations in Western Australian fresh waters was also published by Pen & Potter (1990, 1991a, b, c), Pen *et al.* (1991, 1993), Humphreys & Feinberg (1995), Morgan *et al.* (1995, 1998), Pusey & Bradshaw (1996) and Gill & Morgan (1998), as were the first genetic studies on freshwater fishes in the State (Adams & Humphreys 1993; Storey *et al.* 1995). Taxonomic studies continued during the 1980s and 1990s, with several new Western Australian species described (McDowall & Frankenburg

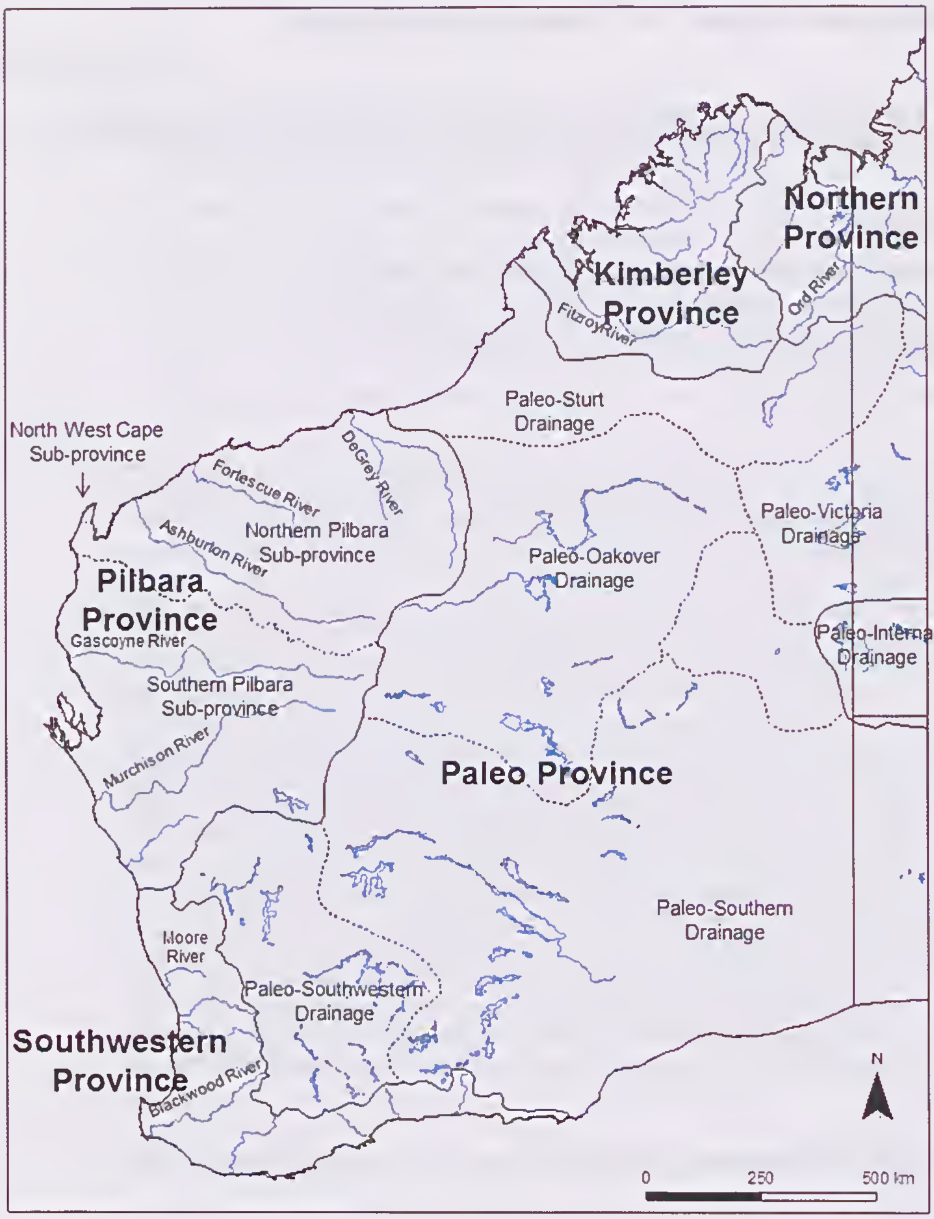

Figure 1 Freshwater fish biogeographical provinces of Western Australia adapted from Unmack (2013).

1981; Hoese & Allen 1983; Allen & Burgess 1990; Allen & Feinberg 1998; Allen & Jenkins 1999). The new millennium saw an increase in ecological and biogeographical studies in the State (Morgan *et al.* 2000, 2003, 2004a; Humphreys 2001; Unmack 2001, 2013; Smith *et al.* 2002; Morgan 2003, 2010; Allen *et al.* 2005; Gill *et al.* 2005; Beesley 2006; Chapman *et al.* 2006; Humphreys *et al.* 2006; Phillips *et al.* 2009; Beatty *et al.* 2010, 2011, 2013a, 2014; Davis *et al.* 2010, 2011, 2013; Ebner & Morgan 2013), culminating in the publication of reviews of fishes of each region (Allen *et al.* 2002; Morgan & Gill 2004; Morgan *et al.* 2004b, 2011a, b, 2014; Beatty & Morgan 2013). With the assistance of genetic tools, new species continue to be identified and described from inland waters of Western Australia, with two described in 2013 (Larson *et al.* 2013; Morgan *et al.* 2013) and many other new species recently identified and awaiting description (Unmack 2013).

Migration categories

For the purpose of this review, the term 'freshwater fishes' encompasses species belonging to the agnathans (jawless fishes), elasmobranchs (cartilaginous fishes) and teleosts (bony fishes) that are obligate inhabitants of fresh waters for some part of their life-cycle. Many teleost fishes that are found within Western Australian fresh waters are known to be, or are likely to be, potamodromous, i.e. they migrate wholly within fresh waters usually for the purpose of breeding, and complete their entire life-cycle within fresh waters (from Myers 1949). However, Myers (1949) discounts the use of this term for small or lateral breeding migrations, such as those "from the stream into the flooded forest during high water" or "the slight movement from a river channel to a shallow sand-bar for spawning". A number of Western Australian species, e.g. *Lepidogalaxias salamandroides*, *Galaxiella nigrostriata* (Black-stripe Minnow) and some populations of *Nannatherina balstoni* (Balston's Pygmy Perch) undertake short, lateral migrations from small pools into inundated riparian vegetation for the purpose of breeding (egg-deposition) (e.g. Pen *et al.* 1993; Morgan *et al.* 1995, 2000), but according to Myers' definition would not constitute being categorised as potamodromous. With the exception of studies by Morgan & Beatty (2006) and Beatty *et al.* (2010, 2014), there are no further studies reporting on potamodromous migrations of fishes in this State. Accordingly, we are unable to assign the obligate freshwater fishes with migratory categories, and for the purpose of this review, they are tentatively labelled as potamodromous in that they all migrate within freshwater to some extent for breeding (Table 1).

Diadromy, a term that Myers (1949) coined for those fishes migrating between the sea and fresh water or at least between one of these biomes and the estuary, is not uncommon in Western Australian fishes and can be further subdivided into anadromy, catadromy or amphidromy (see also McDowall 1997). Anadromy involves an adult migration from the sea to rivers to spawn [e.g. *Geotria australis* (Pouched Lamprey) (Potter *et al.* 1979)], whereas catadromy involves a migration from fresh waters to marine waters for spawning e.g. *Lates calcarifer* (Barramundi). However, some populations of this species may be entirely marine (Moore & Reynolds 1982; Pender & Griffin 1996; McCulloch *et al.* 2005), and those in fresh water generally migrate to the estuary rather than the sea for spawning (categorised as semi-catadromous in Elliott *et al.* (2007)).

Amphidromy was a term developed by Myers (1949) for diadromous fishes "whose migration from fresh water to the sea, or *vice-versa*, is not for the purpose of breeding but occurs regularly at some other definite stage of the life-cycle". McDowall (1997, 2007) refined this definition to include only those fish that emigrate immediately to sea as newly hatched larvae where they grow and feed at sea for a period of a few weeks to months before returning to fresh water as juveniles [(e.g. *Galaxias maculatus* (Common Jollytail) (Chapman *et al.* 2006)]. It should be noted that in rare cases, fishes that are typically amphidromus may have populations that are land-locked and are potamodromous [e.g. *G. maculatus* and *Galaxias truttaceus* (Trout Minnow) see Morgan 2003; Chapman *et al.* 2006; Morgan & Beatty 2006)]. Euryhaline elasmobranchs that enter fresh waters as juveniles, which they use as nursery habitats [e.g. *Pristis pristis* (Thorburn *et al.* 2007; Whitty *et al.* 2009; Morgan *et al.* 2011b)], could be considered amphidromous according to the definition given by Myers (1949). However, based on McDowall's refinement, we note that the few elasmobranchs that mature at sea, pup in estuaries and undertake early juvenile growth in fresh water, do not have a free-swimming larval phase. In this review we categorise these species simply as euryhaline elasmobranchs.

Where available, species-specific life-cycle categories have been assigned to species from information collated from general texts (e.g. Allen *et al.* 2002) or from studies conducted on these species outside of Western Australia [e.g. the semi-anadromous *Megalops cyprinoides* in Coates (1987), Donaldson & Myers (2002), yet considered amphidromous by Myers (1949)]. Elliott *et al.* (2007) defined marine migrants as species that "spawn at sea and often enter estuaries in large numbers particularly as juveniles". Many species fall into this category in Western Australia, with a subset of these continuing their migration through estuaries and into fresh waters. Elliott *et al.* (2007) consider Mangrove Jack (*Lutjanus argentimaculatus*), Milkfish (*Chanos chanos*) and some members of the Mugilidae to be marine migrants; members of the Mugilidae and the above species often occur in fresh waters of Western Australia. 'Marine vagrants' or 'marine stragglers' are other species that spawn at sea and typically enter estuaries only in low numbers (Elliott *et al.* 2007), some of which are occasionally found in fresh waters in Western Australia. We cover the presence of such species within Western Australian freshwater habitats within this review for completeness. Additionally, a number of species that are typically estuarine (or complete their lives within the estuary) but on occasion enter fresh waters are covered in this review; we categorise these as 'estuarine vagrants'. It should be noted that several Western Australian estuarine species are able to complete their life-cycle within fresh waters.

Fishes of the inland waters of Western Australia

It is evident that the inland waters of Western Australia provide critical habitats to species that are found nowhere else. Below we review the current knowledge surrounding the fishes in each ichthyological province of Western Australia. This is important in light of the increasing anthropogenic stressors that this unique fauna is being challenged with, including the major loss of habitat through salinisation, dewatering, river regulation, agricultural activity and climate change (Morgan *et al.* 2003; Beatty *et al.* 2014) and from the impact of an ever increasing alien fauna (Morgan *et al.* 2004b; Beatty & Morgan 2013). This overview collates information from the large body of historical and recent research of the Western Australian 'freshwater fish' fauna, to serve as a reference point for current and future researchers.

Southwestern Province

The Southwestern Province hosts a unique and highly endemic fauna, the highest of any ichthyological province in Australia in terms of the proportions of endemic species (11 of 14), genera and families (Table 1, Figure 2) (Unmack 2013). The province is dominated by species with ancient lineages that are either unique to the south-west region or that have historical links to temperate eastern Australia that were severed due to increasing aridity and formation and uplift of the Nullarbor Plain (Unmack *et al.* 2011).

The most outstanding endemic species is *Lepidogalaxias salamandroides* which belongs to the Lepidogalaxiidae, an endemic family within the Southwestern Province. This remarkable species is one of the world's most unusual teleosts (e.g. Pusey 1989; Morgan *et al.* 2000) and the sole representative of an early divergent lineage within teleost evolution. Estimates put its mean age of divergence from its nearest relatives at ~230 million years ago (Ma) (Betancur *et al.* 2013).

One species of Plotosidae, *'Tandanus' bostocki* (Freshwater Cobbler) is the largest potamodromous fish of the region (reaching over 400 mm total length (TL)) (Beatty *et al.* 2010). This species, incorrectly placed in the genus *Tandanus*, represents an undescribed genus which is one of the earliest branching lineages within freshwater plotosids, and its divergence dates to the early Tertiary (Unmack *et al.* unpub. data). These two endemic groups (*Lepidogalaxias salamandroides* and *'Tandanus'*

Table 1 Native fishes (Agnatha, Chondrichthyes and Osteichthyes) found in the fresh waters of Western Australia. A Roman numeral after the species name indicates different taxa based on molecular data that are yet to be revised taxonomically. An * after the species name indicates that the current taxonomy is incorrect, but it remains unclear as to how many species are present and their distributions. Life-cycle category: An = anadromous fishes, EE = euryhaline elasmobranch, Am = amphidromous species, MM = marine migrants, MV = marine vagrants, EV = estuarine vagrants, C = catadromous fishes, Sc = semi-catadromous, and P = potamodromous fishes (but includes those freshwater obligatory species where migratory information is unavailable). Under Drainage Division, SW = Southwestern Province, P = Pilbara Province, K = Kimberley region, Pa = Paleo Province.

Species name	Common name	Life-cycle category	Drainage Division	Fig. 2 photo #
Geotriidae				
Geotria australis	Pouched Lamprey	An	SW	1
Carcharhinidae				
Carcharhinus leucas	Bull Shark	EE	SW/P/K	2
Pristidae				
Pristis pristis	Freshwater Sawfish	EE	P/K	3
Dasyatidae				
Himantura dalyensis	Freshwater Whipray	EE	K	4
Elopidae				
Elops hawaiiensis	Giant Herring	MV	SW/P/K	–
Megalopidae				
Megalops cyprinoides	Tarpon	MM	P/K	5
Anguillidae				
Anguilla bicolor	Indian Short-finned Eel	C	P/K	6
Clupeidae				
Nematalosa erebi I	Bony Bream	P	K	7
Nematalosa erebi II	Pilbara Bony Bream	P	P	–
Chandidae				
Chanos chanos	Milkfish	MV	P/K	–
Ariidae				
Neoarius graeffei	Lesser Salmon Catfish	MV/EV/P	P/K	8
Neoarius midgleyi	Silver Cobbler	P	K	9
Sciades leptaspis	Triangular Shield Catfish	EV	K	–
Plotosidae				
Anodontiglanis dahli I	Toothless Catfish	P	K	10
Anodontiglanis dahli II	Fitzroy Toothless Catfish	P	K	–
Neosilurus ater	Black Catfish	P	K	11
Neosilurus hyrtlii II	Hyrtl's Tandan	P	K/Pa	–
Neosilurus hyrtlii III	Kimberley Tandan	P	K	12
Neosilurus hyrtlii IV	Pilbara Tandan	P	P	–
Neosilurus sp.	Robe River Catfish	P	P	13
Neosilurus pseudospinosus I	False-spined Catfish	P	K	14
Neosilurus pseudospinosus II	Drysdale False-spined Catfish	P	K	–
Porochilus rendahli	Rendahl's Catfish	P	K	15
'Tandanus' bostocki	Freshwater Cobbler	P	SW	16
Galaxiidae				
Galaxias maculatus	Common Jollytail	Am/P	SW	17
Galaxias occidentalis	Western Minnow	P	SW	18
Galaxias truttaceus	Trout Minnow	Am/P	SW	19
Galaxiella munda	Western Mud Minnow	P	SW	20
Galaxiella nigrostriata	Black-stripe Minnow	P	SW	21
Lepidogalaxiidae				
Lepidogalaxias salamandroides	Salamanderfish	P	SW	22
Mugilidae				
Liza alata	Diamond Mullet	MM	K	–
Liza subviridis	Greenback Mullet	MM	P/K	–
Liza vaigiensis	Diamondscale Mullet	MM	P/K	–
Mugil cephalus	Sea Mullet	MM	SW/P/K	–
Melanotaeniidae				
Melanotaenia australis	Western Rainbowfish	P	P/K/Pa	23
Melanotaenia exquisita	Exquisite Rainbowfish	P	K	24
Melanotaenia gracilis	Slender Rainbowfish	P	K	25

Species name	Common name	Life-cycle category	Drainage Division	Fig. 2 photo #
Melanotaenia nigrans	Black-banded Rainbowfish	P	K	26
Melanotaenia pygmaea	Pygmy Rainbowfish	P	K	27
Melanotaenia sp. Bindoola	NA	P	K	–
Atherinidae				
Craterocephalus cuneiceps	Deep Hardyhead	P	P	28
Craterocephalus helenae	Drysdale Hardyhead	P	K	29
Craterocephalus lentiginosus	Prince Regent Hardyhead	P	K	30
Craterocephalus stramineus II	Strawman	P	K	31
Leptatherina wallacei	Western Hardyhead	EV/P	SW	32
Synbranchidae				
Ophisternon candidum	Blind Cave Eel	–	P	33
Belonidae				
Strongylura krefftii	Freshwater Longtom	P	K	34
Hemiramphidae				
Arrhamphus sclerolepis	Snub-nosed Garfish	MV/EV/P	P/K	35
Ambassidae				
Ambassis macleayi	Macleay's Glassfish	P	K	36
Ambassis sp. Northwest	Northwest Glassfish	P	K	37
Ambassis sp. Fitzroy	Fitzroy Glassfish	P	K	38
Parambassis gulliveri	Giant Glassfish	P	K	39
Latidae				
Lates calcarifer	Barramundi	Sc	P/K	40
Percichthyidae				
Bostockia porosa I	Nightfish	P	SW	41
Bostockia porosa II	Margaret River Nightfish	P	SW	–
Nannatherina balstoni	Balston's Pygmy Perch	P	SW	42
Nannoperca pygmaea	Little Pygmy Perch	P	SW	44
Nannoperca vittata I	Western Pygmy Perch	P	SW	43
Nannoperca vittata II	NA (Margaret River)	P	SW	–
Nannoperca vittata III	NA (South Coast)	P	SW	–
Apogonidae				
*Glossamia aprion**	Mouth Almighty	P	K	45
Leiognathidae				
Leiognathus equulus	Ponyfish	MV	K	–
Lutjanidae				
Lutjanus argentimaculatus	Mangrove Jack	MM	P	46
Gerreidae				
Gerres filamentosus	Threadfin Silverbiddy	MV/EV	P/K	–
Gerres subfasciatus	Roach	MV/EV	P/K	–
Sparidae				
Acanthopagrus butcheri	Black Bream	EV	SW	–
Sciaenidae				
Nibea squamosa	Scaly Croaker	MV	K	–
Toxotidae				
Toxotes chatareus	Seven Spot Archerfish	P	K	47
Toxotes kimberleyensis	Kimberley Archerfish	P	K	48
Terapontidae				
Amniataba caudavittata	Yellowtail Trumpeter	MV/EV/P	P	49
Amniataba percoides	Barred Grunter	P	P/K	50
Hannia greenwayi	Greenway's Grunter	P	K	51
Hephaestus epirrhinos	Long-nose Sooty Grunter	P	K	52
Hephaestus jenkinsi	Western Sooty Grunter	P	K	53
Leiopotherapon aheneus	Fortescue Grunter	P	P	54
Leiopotherapon macrolepis	Large-scaled Grunter	P	K	55
Leiopotherapon unicolor	Spangled Perch	P	P/K/Pa	56
Syncomistes butleri	Butler's Grunter	P	K	57
Syncomistes kimberleyensis	Kimberley Grunter	P	K	58
Syncomistes rastellus	Drysdale Grunter	P	K	59
Syncomistes trigonicus	Long-nose Grunter	P	K	60

Table 1 (cont.)

Species name	Common name	Life-cycle category	Drainage Division	Fig. 2 photo #
Eleotridae				
Hypseleotris aurea	Golden Gudgeon	P	P	61
Hypseleotris compressa	Empire Gudgeon	EV/Am/P	P/K	62
Hypseleotris ejuncida	Slender Gudgeon	P	K	63
Hypseleotris kimberleyensis	Barnett River Gudgeon	P	K	64
Hypseleotris regalis	Prince Regent Gudgeon	P	K	65
Kimberleyeleotris hutchinsi	Mitchell Gudgeon	P	K	66
Kimberleyeleotris notata	Drysdale Gudgeon	P	K	–
Milyeringa veritas	Blind Gudgeon	–	P	67
Milyeringa justitia	Barrow Gudgeon	–	P	–
*Mogurnda mogurnda**	Northern Trout Gudgeon	P	K	68
*Mogurnda oligolepis**	Kimberley Mogurnda	P	K	69
Oxyeleotris lineolata	Sleepy Cod	P	K	70
Oxyeleotris selheimi	Giant Gudgeon	P	K	71
Kurtidae				
Kurtus gulliveri	Nurseryfish	EV	K	72
Gobiidae				
Afurcagobius suppositus	South-west Goby	EV/P	SW	73
Glossogobius giuris	Flathead Goby	P	P/K	74
Pseuogobius olorum	Blue-spot Goby	EV/P	SW/P	75
Scatophagidae				
Scatophagus argus	Spotted Scat	MV	P/K	–
Selenotoca multifasciata	Banded Scat	MV	P/K	–
Soleidae				
Leptachirus triramus	Tailed Sole	P	K	76
Tetraodontidae				
Marilyna meraukensis	Merauke Toadfish	MV/EV	K	–

bostocki) represent ancient and unusual lineages that have persisted in this Province and represent important legacies in the evolution of Australian fishes. Most other freshwater fishes in the Southwestern Province have old relationships to species in temperate eastern Australia that were severed due to the formation and uplift of the Nullarbor Plain and increasing aridity (Unmack *et al.* 2011). This includes seven endemic species of Percichthyidae (including two endemic genera, *Bostockia* and *Nannatherina*) and five species of Galaxiidae, three of which are endemic to the Province (Table 1).

Divergences among genera and species within the Southwestern Province span a range of dates. The origins of western percichthyids are estimated to be older than 40 Ma, with some genetic exchange between eastern and western Australian species occurring until around 14 Ma (Unmack *et al.* 2011). The galaxiid genus *Galaxiella* is represented by two species in the Province, *Galaxiella nigrostriata* and *Galaxiella munda* (Western Mud Minnow) which are estimated to have diverged from their eastern Australian relatives around 34 Ma (Unmack *et al.* 2012). The endemic *Galaxias occidentalis* (Western Minnow) diverged from eastern relatives around 15 Ma (Burridge *et al.* 2011). The split between the two endemic *Galaxiella* species has been dated at a mean age of 22.5 Ma (Unmack *et al.* 2012), while deeper divergences within the *Nannoperca vittata* (Western Pygmy Perch) species complex (comprising four species) began around 10 Ma (Unmack *et al.* 2011). Divergence between each species pair in the 'vittata' species complex, as well as the species pair within *Bostockia porosa* (Nightfish) occurred more recently at an estimated mean age of around 1–3 Ma (Unmack *et al.* unpub. data). One taxon belonging to the 'vittata' group was recently described as *Nannoperca pygmaea* (Little Pygmy Perch) and has a small biogeographical range compared to at least two of its congeners (Morgan *et al.* 2013).

The remaining species usually have some interactions between fresh and marine environments. The two remaining galaxiids, *Galaxias maculatus* and *Galaxias truttaceus*, both have an amphidromous life history in eastern Australia and whilst this is sometimes the case for *G. maculatus* in the Southwestern Province, a potamodromous life-cycle is more typical (Humphries 1989; Morgan 2003; Chapman *et al.* 2006; Morgan & Beatty 2006; Morgan *et al.* 2006).

The agnathan *Geotria australis* is anadromous; adults spawn in fresh water and the ammocoete larvae spend the first few years of their life in these habitats, before migrating into marine habitats feeding parasitically and growing (Potter *et al.* 1979). Some species that are typically estuarine species, such as *Leptatherina wallacei* (Western Hardyhead), *Pseudogobius olorum* (Blue-spot Goby) and *Afurcagobius suppositus* (South-west Goby) (Prince & Potter 1983; Potter & Hyndes 1999) have recently colonised many of the upstream reaches of the Province's larger river systems as a result of secondary salinisation (Morgan *et al.* 1998, 2003). However, each of these species also occurs naturally within a few fresh water coastal lakes and within the estuaries (Morgan *et al.* 1998). *Mugil cephalus* (Sea Mullet) is found in freshwater reaches of a few rivers, but generally only in very low numbers compared to estuaries. *Acanthopagrus butcheri* (Black Bream), which we categorise as an 'estuarine vagrant', is only very occasionally found in the non-tidal waters of Western Australia, although it occurs in many estuaries of the region (Sarre *et al.* 2000).

There are a number of reports of *Carcharhinus leucas* (Bull Shark) from the estuaries of the Swan, Canning, Blackwood and Collie rivers, but none appear to make the transition into fresh waters, possibly due to seasonality of parturition in the species being different to the defined high flow regimes of the rivers resulting from the Mediterranean climate of the Province. Alternatively, natural and artificial barriers may play a role in limiting access to the upstream reaches of rivers. In recent times, a single *Hypseleotris compressa* (Empire Gudgeon) was found in a south-west river, although this record probably resulted from a southerly larval drift from the Pilbara Province, where this species is commonly encountered (Morgan & Gill 2004; Morgan & Beatty 2008). It remains to be seen whether this species naturally establishes populations in the Southwestern Province.

The highest species richness in the Province is found within the Blackwood River catchment (including the Scott River), which is also the largest river by discharge. It hosts the lamprey, six freshwater fishes and three estuarine species that have colonised large sections of this salinised system. The Margaret River is also an important basin which appears to have endemic species within the *Bostockia porosa* and *Nannoperca vittata* species groups (Unmack 2013). Most species in the Southwestern Province are concentrated in the coastal portion of the south-western most river basins in the region that experience the highest rainfalls, from approximately Albany to Perth. Outside this higher rainfall belt, species richness drops sharply with the fauna dominated by those species tolerant of drier, harsher environments such as *Nannoperca vittata*, *Galaxias occidentalis* and *Pseudogobius olorum*. These three species are the most widespread native fishes in the Southwestern Province; the first two species are found east to Waychinnicup River and north to Irwin River (south of Geraldton), while the latter species occurs east of Esperance and north into the Murchison River in the Pilbara Province.

Many of the native fishes of this region have undergone extensive range contractions, and in some catchments certain species have become restricted to a few remaining suitable habitats (Morgan *et al.* 1998; Galleotti *et al.* 2010; Beatty *et al.* 2014). Range declines were recently formally recognised with the listing of several species under both Federal and State endangered species legislation, and this Province has the highest proportion of threatened fishes in the State (Table 2). This is not surprising given that it is home to most of the State's human population and has the highest proportion of anthropogenic impacts. Anthropogenic stressors impacting fishes in the rivers and lakes of the region include salinisation, eutrophication, river regulation, alien fishes and, more recently, climate change (Morgan *et al.* 2003, 2004b; Beatty *et al.* 2011, 2013, 2014; Morrongiello *et al.* 2011; Beatty & Morgan 2013). Declining rainfall and surface flows, and subsequent reductions in groundwater levels, are impacting fishes, with the region one of the most seriously threatened by climate change (Beatty *et al.* 2014).

Pilbara Province

The Pilbara Province includes all river basins from the Irwin River in the south to the De Grey River in the north (Figure 1) (Morgan & Gill 2004). The northern boundary abuts the Great Sandy Desert which has largely isolated this Province from other parts of northern Australia. Consequently, the freshwater fishes in this province are either local endemics (6 species) or have extensive distributions across much of northern Australia (4 species; Table 1). There are no shared freshwater fish species with the Southwestern Province, although some estuarine species are shared, such as *Acanthopagrus butcheri* and *Pseudogobius olorum*, as far north as the Murchison River (Table 1). Distinct patterns in the distribution of fish species in the Pilbara Province resulted in the recognition of three sub-provinces, namely the Southern Pilbara, Northern Pilbara, and North West Cape (Figure 1) (Morgan & Gill 2004).

The most unusual endemic fishes of the Pilbara are found in the subterranean waters in North West Cape Sub-province. Two species of cave gudgeon occur allopatrically. *Milyeringa veritas* (Blind Gudgeon) occurs on the mainland at Cape Range Peninsula while the newly described *Milyeringa justitia* (Barrow Cave Gudgeon) is restricted to Barrow Island (Figure 2) (Humphreys & Adams 1991; Humphreys 1999, 2001; Humphreys *et al.* 2013; Larson *et al.* 2013). Both species share their habitat with *Ophisternon candidum* (Blind Cave Eel), although it is likely that the eels on Barrow Island also represent an additional endemic species given the divergence of the two *Milyeringa* species. There are also reports of additional *Ophisternon* populations in groundwater systems in the Robe basin (Larson *et al.* 2013). The subterranean habitats where these species occur are devoid of light except close to openings to the surface. There are freshwater caves as well as anchialine ecosystems which comprise fresh to brackish ground waters overlying sea water, some of which are tidal with salinities ranging from 0.3 to 34 ppt (Humphreys 2001). These unusual characteristics make it impossible to categorise the subterranean fauna as freshwater, estuarine or marine as they live under the terrestrial surface. This environment represents one of only a few examples of sympatric cave fish species in the world (Proudlove 2006).

The surface dwelling freshwater fish fauna is dominated by a relatively small number of species that can survive in the extreme environments of the Pilbara where rivers experience massive flooding following cyclones and limited water availability during dry times. The fauna consists of three fishes endemic to the province; *Craterocephalus cuneiceps* (Deep Hardyhead) and *Hypseleotris aurea* (Golden Gudgeon) are primarily restricted to southern rivers, but with the former having a disjunct northern population in the De Grey River (Morgan & Gill 2004; Allen *et al.* 2005), whilst *Leiopotherapon aheneus* (Fortescue Grunter) is restricted to a few Northern Sub-province rivers (Morgan and Gill 2004). A possible new species of *Neosilurus* catfish from the Robe River may also be endemic although it has not been captured for a number of years and the Robe River is predicted to have the highest freshwater fish extinction rate on the planet under future climate change scenarios (Tedesco *et al.* 2013).

Table 2 The fishes in non-tidal waters of Western Australia that are listed by: the International Union for the Conservation of Nature (IUCN); the Australian Federal Government (Environment Protection and Biodiversity Conservation Act (EPBC Act 1999)); or the Western Australian Government (Wildlife Conservation Act 1950 (WCA Act 1950) and the Fish Resources Management Act 1994 [FRMA 1994]). Also included is the Australian Society for Fish Biology's (ASFB) list. NT = near threatened, CE = critically endangered, DD = data deficient, LR/NT = lower risk/near threatened, LR/LC = lower risk/least concern, LC = least concern, V = vulnerable, Schedule 1 = fauna that is rare or is likely to become extinct, Priority 1 = poorly-known species (on threatened lands), Priority 2 = poorly-known species (on conservation lands), Priority 3 = poorly-known species (some on conservation estates), Priority 4 = rare, near threatened and other species in need of monitoring, FP = fully protected.

Species name	IUCN	EPBC 1999	WCA 1950	FRMA 1994	ASFB
Geotriidae					
Geotria australis	–	–	Priority 1	–	–
Carcharhinidae					
Carcharhinus leucas	NT	–	–	–	–
Pristidae					
Pristis pristis	CE	V	Priority 3	FP	CE
Dasyatidae					
Himantura dalyensis	DD	–	–	–	V
Anguillidae					
Anguilla bicolor	NT	–	–	–	–
Galaxiidae					
Galaxias truttaceus	–	CE	Schedule 1	–	CE
Galaxiella munda	LR/NT	–	Schedule 1	–	–
Galaxiella nigrostriata	LR/NT	–	Priority 3	–	–
Lepidogalaxiidae					
Lepidogalaxias salamandroides	LR/NT	–	–	–	–
Melanotaeniidae					
Melanotaenia exquisita	DD	–	–	–	–
Melanotaenia gracilis	LR/NT	–	–	–	–
Melanotaenia pygmaea	LR/NT	–	Priority 2	–	–
Atherinidae					
Craterocephalus helenae	LR/NT	–	Priority 2	–	–
Craterocephalus lentiginosus	LR/NT	–	Priority 2	–	–
Synbranchidae					
Ophisternon candidum	DD	–	Schedule 1	–	V
Ambassidae					
Ambassis macleayi	LC	–	–	–	–
Percichthyidae					
Nannatherina balstoni	DD	V	Schedule 1	–	V
Nannoperca pygmaea	–	–	–	–	CE
Terapontidae					
Hannia greenwayi	DD	–	Priority 1	–	–
Hephaestus epirrhinos	LR/NT	–	Priority 2	–	–
Leiopotherapon aheneus	LR/NT	–	Priority 4	–	–
Leiopotherapon macrolepis	LC	–	Priority 2	–	–
Syncomistes kimberleyensis	LR/NT	–	–	–	–
Syncomistes rastellus	LR/NT	–	Priority 2	–	–
Eleotridae					
Hypseleotris aurea	LR/LC	–	Priority 2	–	–
Hypseleotris ejuncida	LR/NT	–	–	–	–
Hypseleotris kimberleyensis	LR/NT	–	–	–	–
Hypseleotris regalis	LR/NT	–	–	–	–
Kimberleyeleotris hutchinsi	–	–	Priority 2	–	–
Kimberleyeleotris notata	–	–	Priority 2	–	–
Milyeringa justitia	–	–	Schedule 1	–	–
Milyeringa veritas	DD	V	Schedule 1	–	V
Kurtidae					
Kurtus gulliveri	LC	–	–	–	–

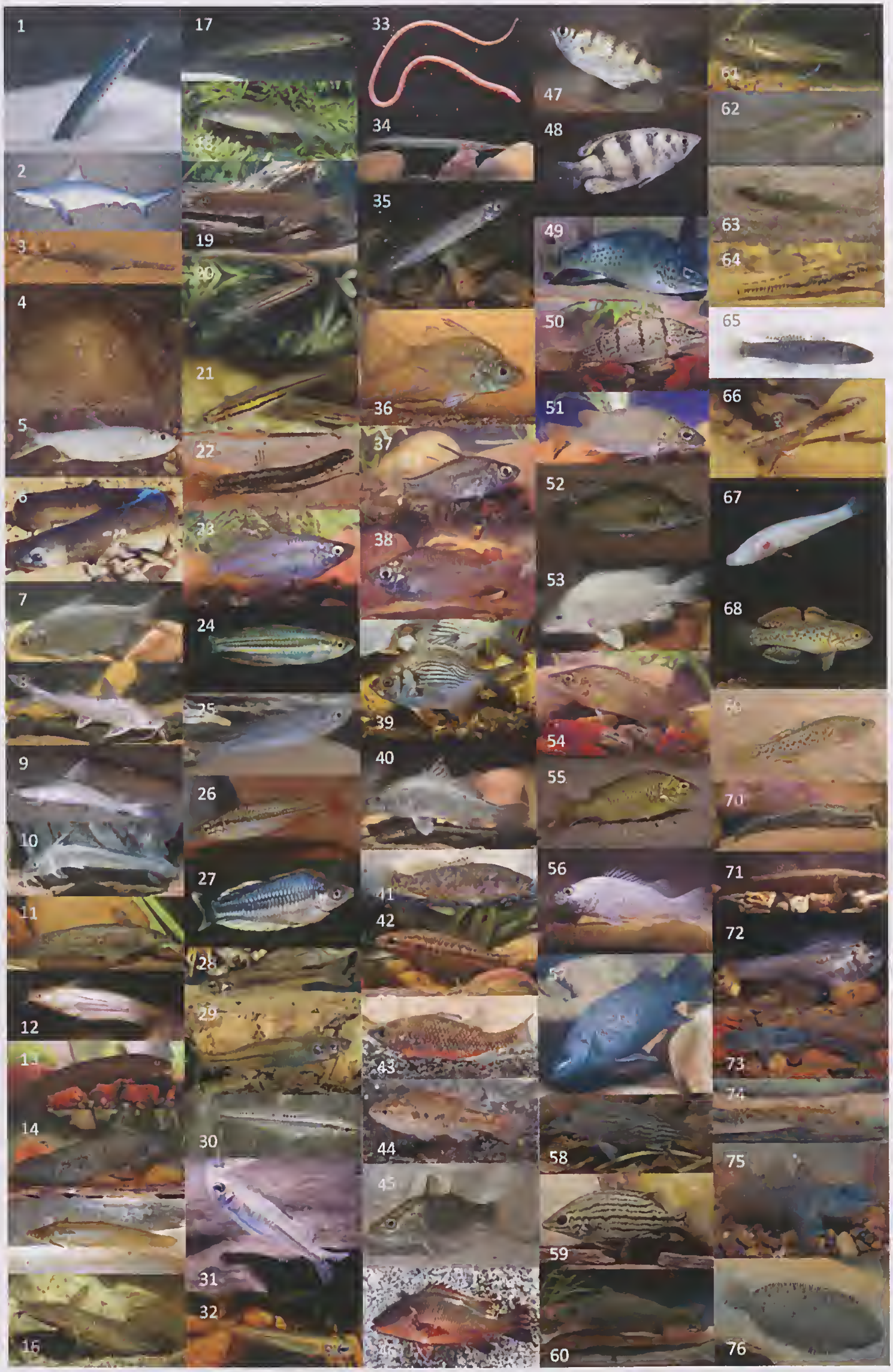

Figure 2 Fishes in fresh water habitats of Western Australia that spend all, or part of, their life-cycle in fresh water. Not pictured are the marine migrants, marine vagrants, estuarine vagrants, undescribed species, *Milyeringa justitia* or *Kimerleyeleotris notata*. Please refer to Table 1 for species names. Photographs by D. Morgan, M. Allen, G. Allen, S. Beatty, S. Visser and B. Ebner.

The remaining freshwater species are all widespread across northern Australia, although Pilbara populations tend to be genetically distinct with some differences sufficiently large to suggest they represent distinct (and thus endemic) species (Unmack 2013). For example, Pilbara populations of *Nematalosa erebi* (Bony Bream) and *Neosilurus hyrtlii* (Hyrtl's Tandan), two of Australia's most widespread freshwater fishes, both appear to be new species according to allozyme, mitochondrial and nuclear DNA studies (Unmack 2013; M. Adams & P. Unmack unpubl. data), and warrant closer morphological examination. Pilbara populations of *Melanotaenia australis* (Western Rainbowfish) are also genetically distinct to populations elsewhere in northern Australia (Young *et al.* 2011; Unmack *et al.* 2013). While most Pilbara fishes have phylogenetic relationships to other species from northern Australia, one exception is *Craterocephalus cuneiceps*, which, based on limited evidence, appears to be more closely related to central and eastern Australian *Craterocephalus* species than northern species (Unmack & Dowling 2010).

In contrast to the Southwestern Province, there are more estuarine and marine vagrants occurring in the non-tidal waters of the Pilbara Province (Table 1). At least 13 species of estuarine or marine vagrants are found in fresh waters of the Province, and in some habitats they have been recorded to comprise between 5 and 10% of the total fish numbers (see also Morgan & Gill 2004; Ebner & Morgan 2013). Some species also appear capable of breeding within either estuarine or fresh waters and are troublesome for simplistic migratory classification schemes; they could be classed as either estuarine vagrants that colonise fresh waters or as 'freshwater fishes' in the case of some populations. Examples include *Pseudogobius olorum* and *Hypseleotris compressa*.

Diadromous fishes of the Pilbara Province include *Lutjanus argentimaculatus* (Mangrove Jack), *Megalops cyprinoides* (Tarpon), *Carcharhinus leucas* and *Pristis pristis* (Morgan & Gill 2004; Ebner & Morgan 2013). The only confirmed records of the latter species are from the Ashburton River below a barrier built to stop the upstream incursion of tidal water, but they have also occasionally been reported from the De Grey River (Morgan unpubl. data). Catadromous species include *Anguilla bicolor* (Indian Short-finned Eel), while *Lates calcarifer* (Barramundi) is considered to be semi-catadromous.

Future impacts to the habitats and fishes of the region are likely to result from the impacts of climate change and from dewatering of habitats during mining and through water abstraction (Tedesco *et al.* 2013). As an example, Tedesco *et al.* (2013) predicted that freshwater fish extinction rates within river basins within the Northern Pilbara Sub-province will be amongst the highest on the globe. Incredibly, the authors predicted that six of the rivers within the Northern Pilbara Sub-province will be in the top 12 rivers globally to suffer the highest extinction rates due to water availability shrinkage from climate change. These include the Robe (ranked 1), Sherlock (3), Fortescue (4), Yule (6), Ashburton (7) and De Grey (12) rivers. Therefore, the Pilbara warrants far more research and management attention than it is receiving to halt imminent (and possibly additional) extinctions.

Kimberley and Northern Provinces

For the sake of convenience we discuss the fauna of these two provinces together as the "Kimberley region" as only a limited portion of the Northern Province occurs within Western Australia (Figure 1). The division of these two provinces is primarily based on the presence of a number of fishes endemic to the Kimberley Province (19 species), rather than species present in the Northern Province but absent from Kimberley Province [with a couple of key exceptions, i.e. *Craterocephalus stramineus* (Strawman) and *Parambassis gulliveri* (Giant Glassfish)]. Furthermore, the boundary between the two provinces is somewhat arbitrary, as currently defined river basins such as the King George and Berkeley remain poorly sampled, such that the boundary cannot be more reliably determined (Morgan *et al.* 2011a; Unmack 2013).

The Kimberley region is a poorly known area of high fish species richness (48 species; Table 1). Many rivers are difficult to access or access is only available to a limited portion of the river basin. As a result, the taxonomy of many Kimberley fishes is uncertain. Many groups appear to contain multiple cryptic species, some of which are widespread while others have highly restricted distributions. High endemicity in the Kimberley is likely a result of the rugged topography; many rivers are characterised by deep gorges and waterfalls which limit migratory movement and exclude diadromous species.

The Kimberley region lacks any highly unusual or particularly old relictual endemic freshwater groups (as is the case in most of northern and eastern Australia). Only two genera are endemic (*Hannia* and *Kimberleyeleotris*). However, many families have high species richness and endemism compared to most regions of the continent. The major families include the Terapontidae (10 species), Eleotridae (10 species), Plotosidae (8 species), Melanotaeniidae (6 species), Ambassidae (4 species), and Toxotidae (2 species) (Table 1, Figure 2) (Morgan *et al.* 2011a; Unmack 2013). Although all groups appear to be primarily related to species found across northern Australia, a key difference is that much of northern Australia east of Darwin was potentially more interconnected during low sea levels, as were basins such as the Daly, Victoria and Ord (Unmack 2001). The shorter catchments and rugged topography around the Kimberley Province appears to have isolated elements of the fauna from eastern regions, leading to divergence through isolation over long time periods. Few molecular clock approaches or phylogenies have been published on Kimberley region fishes, but a mean divergence of 20.5 Ma has been estimated to have occurred between the sister species *Craterocephalus helenae* (Drysdale River Hardyhead) and *Craterocephalus marianae* (from western Arnhemland) which represents the earliest branching lineage (mean age of 37.5 Ma) within the "eyresii group" (Unmack & Dowling 2010). In rainbowfishes, the "nigrans" group (which is endemic to northern Australia) had its mean divergence from its sister lineage (the "australis" group) 12 Ma, with modern species diversifying over the last 6 Ma. Within the "nigrans" group, species endemic to the Kimberley Province such as *Melanotaenia pygmaea* (Pygmy Rainbowfish) and *Melanotaenia gracilis* (Drysdale Rainbowfish) diverged from their sister lineages/species around 5 and 1.5 Ma, respectively (Unmack *et al.* 2013).

The total number of obligate freshwater fish species in this region currently stands at 48 species, but is likely to increase with further exploration and the implementation of genetic studies, especially in groups like *Mogurnda* and *Glossamia*. Numerous diadromous fishes are found within the Kimberley region, including seven that are shared with the Pilbara Province and additionally *Himantura dalyensis* (Freshwater Whipray) (Morgan *et al.* 2004a; Marzullo *et al.* 2011). The catadromous (i.e. *Anguilla bicolor*) and semi-catadromous (i.e. *Lates calcarifer*) fishes found in the Pilbara are also found within the Kimberley, and these provinces comprise the Australian range of *Anguilla bicolor* (Morgan & Gill 2004; Morgan *et al.* 2004a, 2011a). We document 15 marine and estuarine vagrants or marine migrants within the Kimberley region and a further two species that are able to breed within either marine, estuarine or fresh waters (Table 1). A further two conservation dependent euryhaline elasmobranchs [*Glyphis garricki* (Northern River Shark) and *Glyphis glyphis* (Speartooth Shark)] are known from Western Australian estuaries, but neither of these have been recorded within non-tidal inland waters in Western Australia (see Thorburn & Morgan 2004; Morgan *et al.* 2011b).

Paleo Province

Very little is known about the fishes of the Paleo Province. This vast area covers almost half of Australia, although none of it drains to the ocean due to arid conditions and a lack of larger coordinated drainages (Figure 1). The Paleo Province is divided up into sub-provinces or "drainages" based on likely former connections and drainage directions that have had limited connectivity from at least the mid Miocene (Van de Graaff *et al.* 1977; Unmack 2001, 2013). Despite this apparent extreme isolation and the aridity of the region, some records of fish exist, including three species in the Sturt Creek/Lake Gregory system [Paleo Sturt Drainage; *Leiopotherapon unicolor* (Spangled Perch), *Melanotaenia australis* and *Neosilurus hyrtlii*)] (Walker 2009). Populations of the latter two species are genetically related to populations from adjacent Kimberley drainages (Unmack *et al.* unpubl. data). Museum databases indicate that *Leiopotherapon unicolor* and *Melanotaenia australis* have been collected from the Ruddall River system (Paleo Oakover Drainage). There are also records of *Leiopotherapon unicolor* in the Lake Boonderroo/Ponton Creek system (Paleo Southern Drainage), and the introduced *Gambusia holbrooki* and *Carassius auratus* (Goldfish) from several other locations within the Paleo Province (see Morgan *et al.* 2004b). The introduced crayfish *Cherax destructor* (Yabby) is found in a few localities (see Beatty *et al.* 2005). Specific areas within the Paleo Province require dedicated survey and study due to the paucity of data that exists for this area.

Threatened fishes of Western Australia

Western Australian fishes are placed on various conservation lists at international (1), national (2) and state level (3) (see Table 2), but there is little consistency between the different lists and categories. Only one species from WA appears on all five lists (*Pristis pristis*), and three species appear on at least one list at the international, national and state levels (Table 2). Many freshwater fish species in Western Australia are imperilled as evidenced by the total of 33 listed species (Table 2), including two Critically Endangered species, *Pristis pristis* and *Galaxias truttaceus*, according to the IUCN and EPBC lists, respectively. It is important to consider that many of Western Australia's freshwater fishes are naturally rare or have very restricted distributions, mainly as a consequence of evolving in systems that became isolated long ago, e.g. *Melanotaenia pygmaea* (Pygmy Rainbowfish), *Hypseleotris ejuncida* (Slender Gudgeon), *Hypseleotris kimberleyensis* (Barnett River Gudgeon) and *Hypseleotris regalis* (Prince Regent Gudgeon). There is also a disconnect between the true status of some species and their categorisation on conservation lists, e.g. *Kimberleyeleotris notata* (Drysdale Gudgeon), is known only from two specimens at a single locality, but is only acknowledged as a Priority 2 species under the State's Wildlife Conservation Act 1950. Of the two fishes that were first described in 2013 (*Milyeringa justitia* and *Nannoperca pygmaea*), both of which are extremely rare, range restricted and threatened by anthropogenic stressors, only *M. justitia* is officially recognised as threatened, but only on one government list, while *N. pygmaea* is listed as Critically Endangered by the Australian Society for Fish Biology (Lintermans 2013). Unless nominations are submitted, or species are reviewed, these lists may only serve as a reminder of the threatened nature of many species.

Alien fishes in Western Australia

Regrettably, the Southwestern Province now supports a range of alien fishes that compete with native species for habitat and resources, and the number is likely to increase with new species being reported and existing alien fishes (and their associated alien parasites) spreading naturally and through human activities (Morgan & Gill 2001; Morgan *et al.* 2002, 2004b; Morgan 2003; Lymbery *et al.* 2010, 2014; Beatty & Morgan 2013; Duffy *et al.* 2013). In a recent review by Beatty & Morgan (2013), 13 species were identified as having developed self-maintaining populations from wild systems in the Southwestern Province. This study identified that the majority were 'climatically mismatched' and 80% of recent introductions were aquarium species. They projected that this trend was likely to continue due to projected climate change. Indeed, consistent with their prediction, another tropical aquarium cichlid species was recently reported by Duffy *et al.* (2013).

To the best of our knowledge, the Northern Pilbara Sub-province is currently free of introduced fishes. Within the North West Cape Sub-province *Poecilia reticulata* (Guppy) has been introduced into some sites housing cave fishes, while the Southern Pilbara now houses *Oreochromis mossambicus* (Mozambique Mouthbrooder or Tilapia) in estuarine and freshwaters of the Chapman, Gascoyne, Minilya and Lyndon rivers (Morgan & Gill 2004; Morgan *et al.* 2004b; Maddern *et al.* 2007). *Gambusia holbrooki* (Eastern Mosquitofish) plagues rivers south of, but not including the Murchison River, while *Xiphophorus hellerii* (Swordtail) occurs within the Irwin River (Morgan & Gill 2001; Maddern *et al.* 2011).

The only record of alien fish in the Kimberley region is *Gambusia holbrooki* near Beagle Bay (Morgan *et al.* 2004b). The crustacean *Cherax quadricarinatus* (Redclaw Crayfish), which is otherwise widespread across northern Australia, has been introduced within the Ord River in the Northern Province (Doupé *et al.* 2004) and more recently into the Harding River of the Pilbara Province (Morgan *et al.* 2014). The recent colonisation by the cane toad (*Rhinella marina*) from the Northern Province will undoubtedly have adverse effects on aquatic fauna in the Kimberley region.

PRIORITIES FOR RESEARCH AND MANAGEMENT

The non-tidal inland waters of Western Australia contain 102 indigenous species of fish, of which one is a jawless fish of the Agantha, three are cartilaginous Elasmobranchii, and the remainder are bony fishes (Teleostei). The agnathan has a circum-polar distribution in the Southern Hemsiphere, and in Western Australia is restricted to the cooler, non-salinised streams of the Southwestern Province. Two of the elasmobranchs are widespread in temperate and tropical waters of the world (*Pristis pristis* and *Carcharhinus leucas*) (Last & Stevens 2009; Morgan *et al.* 2011b), whereas the third species, *Himantura dalyensis,* appears to have a patchy distribution within northern Australian and southern Papua New Guinea waters that are north and west of (and inclusive of) the Fitzroy River in the Kimberley (Morgan *et al.* 2004a; Last & Manjaji-Matsumoto 2008). A further two endangered euryhaline elasmobranchs are known from Western Australian estuaries (i.e. *Glyphis* spp.) but as yet have not been recorded in non-tidal inland waters in the State (Thorburn & Morgan 2004; Morgan *et al.* 2011b).

Conservation of Western Australia's inland fishes

Almost one-third of fishes that are found in Western Australian inland waters are listed as Threatened or Data Deficient. Importantly, no fish species is known to have gone extinct in the wild in Western Australia, but populations have been lost, which is an irreversible trend when noting the genetic isolation of many populations. For example, *Nannatherina balstoni* has been extirpated from a number of river systems, and to 're-stock' from elsewhere is not necessarily going to revive the species, for reasons that are beyond the scope of this overview, but which may include compromising genetic lineages, introductions of parasites, or most importantly that the stressors on those systems that led to the decline of the species in the first instance (from declines in habitat and water quality, and introduced species) render them unsuitable for re-establishment. The streamlining of threatened species lists and assessments is required, which will lead to a better understanding of the priority species, and the threats to each.

Migration patterns, habitats and priorities for research and management

Although the information on individual species migration patterns is limited, it is clear that the Pilbara and Kimberley provinces are utilised to a higher degree by diadromous fishes than the Southwestern Province. Furthermore, marine vagrants and marine migrants are also more likely encountered in the fresh waters of the more northerly rivers of Western Australia. Importantly from a global perspective, parts of the Kimberley are important nursery areas for endangered euryhaline elasmobranchs, with many such habitats having been lost elsewhere in these species' distributional ranges. Several teleost species are able to complete their life-cycle in either fresh, estuarine or marine waters. An example is *Neoarius graeffei* (Lesser Salmon Catfish), which is common in coastal waters, estuaries and fresh waters in the Kimberley and Pilbara provinces. Others, which may be considered to be amphidromous in some populations, are known to have potamodromous 'landlocked' populations in the Southwestern Province, namely, *Galaxias maculatus* and *Galaxias truttaceus* (Morgan 2003; Chapman *et al.* 2006; Morgan & Beatty 2006). Some species are known to occupy very small disjunct habitats and do not appear to migrate far; the scale of their migrations can probably be defined in metres [e.g. *Lepidogalaxias salamandroides* and *Galaxiella nigrostriata* are two species that aestivate and appear to remain in isolated ephemeral peat swamps (Pusey 1989; Morgan *et al.* 2000; Smith *et al.* 2002; Galleotti *et al.* 2010)].

Approximately 70% of the species listed in inland Western Australian waters are restricted to fresh waters. Many of these are endemic to the State, with the Southwestern Province having the highest proportion of endemic freshwater fishes on the continent, and the proportion of endemic fishes is set to rise following the descriptions of cryptic species (Unmack 2013). The region, however, also has a high concentration of alien

Table 3 Established alien fishes of Western Australian wild ecosystems. SW = Southwestern Province, P = Pilbara Province, K = Kimberley Province, Pa = Paleo Province (after Allen *et al.* 2002; Morgan *et al.* 2004b; Beatty & Morgan 2013; Duffy *et al.* 2013; Unmack 2013).

Species name	Common name	Drainage Division
Plotosidae		
Tandanus tandanus	Freshwater Catfish	SW
Salmonidae		
Oncorhynchus mykiss	Rainbow Trout	SW
Salmo trutta	Brown Trout	SW
Cyprinidae		
Carassius auratus	Goldfish	SW/Pa
Cyprinus carpio	Carp	SW
Puntius conchonius	Rosy Barb	SW
Poeciliidae		
Gambusia holbrooki	Eastern Mosquitofish	SW/P/K/Pa
Phalloceros harpagos	One-spot Livebearer	SW
Poecilia reticulata	Guppy	P
Xiphophorus hellerii	Swordtail	SW/P
Percidae		
Perca fluviatilis	Redfin Perch	SW
Cichlidae		
Geophagus brasiliensis	Pearl Cichlid	SW
Oreochromis mossambicus	Mozambique Mouthbrooder	P
Percichthyidae		
Macquaria ambigua	Golden Perch	SW
Terapontidae		
Bidyanus bidyanus	Silver Perch	SW
Leiopotherapon unicolor	Spangled Perch	SW

fishes (Table 3) and this is a figure that will also inevitably increase with further incursions. While escapees from the ornamental industry have contributed to most new species introductions in Western Australia in recent times, there is growing pressure to increase aquaculture and recreational fishing opportunities; noting that one such example is the historial, ongoing, yet controversial stocking of Northern Hemisphere salmonids into Southwestern Province ecosystems.

A list of broad priorities for research and management of Western Australia's inland fishes include:

- Conservation of fishes in the Southwestern Province, particularly with regard to anthropogenic stressors and climate change.
- Conservation of fishes in the Pilbara Province, particularly with regard to climate change, water extraction, mining and alien fishes.
- Conservation of euryhaline elasmobranchs, particularly in the Kimberley which supports globally significant habitats for the Freshwater Sawfish (*Pristis pristis*)
- Audits of drainages lacking sufficient biodiversity surveys, e.g. Paleo Province, much of the Kimberley Province and parts of the Pilbara Province.
- Aligning threatened species lists, and developing a process for streamlining faunal assessments.
- Description of new taxa in the Southwestern, Pilbara and Kimberley provinces.
- Developing a strategy for the targeted control of alien or translocated fishes.

CONCLUSIONS

Of the 102 species of fish found in Western Australia's freshwater ecosystems, some 66 are obligate species, while many diadromous fishes also occur here. Many species are imperilled, and it is clear that in time, new species will be described, including, but by no means limited to, those species highlighted here as being new to science, e.g. *Nannoperca* spp., *Nematalosa* sp. and *Neosilirus* sp. What is also clear is that habitats will be lost and there will be incursions of alien species, none of which will be beneficial to maintaining the status quo of our unique yet often unheralded 'freshwater' fish fauna. Much more attention is warranted in terms of research and management on the fishes outside of the Southwestern Province, particularly the Pilbara, to help prevent extirpations of the more unique fishes.

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An Australian science communication case study based on recovery of the endangered fish red-finned blue-eye, *Scaturiginichthys vermeilipinnis*

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Despite the accepted need for better communication of science and research to non-scientific audiences, peer reviewed papers remain the most common – and frequently the only – method by which research results are communicated. Continuation of this practice in isolation is unlikely to present the results to a wider audience because the majority of non-scientific readers do not consult scientific journals. In this case study the methods used to promote a project concerning the conservation of a small endangered fish from the Australian semi-arid zone are discussed and recommendations are made regarding using such methods more widely. The problem of evaluating such strategies is alluded to, as this is most-often a subjective exercise, and as such difficult to quantify using traditional measurement methods. Results from a small survey of journalists and educators are also presented in order to demonstrate the most important features a science story needs in order to be communicated successfully to a general audience. The case study demonstrates that harnessing a range of communication media (radio, television, internet, magazines, books, public speaking and formal papers) combined with a spatial approach (local, regional, national and international) is a sensible way to garner support and encourage interest in what are often esoteric and obscure research endeavours.

KEYWORDS: science communication, Edgbaston, Great Artesian Basin springs, Lake Eyre Basin

INTRODUCTION

There is a recognised need for scientists to engage with and communicate their work to the general public (Hobbs & Wills 1998; Jacobson 1999; Jacobson *et al.* 2006), and this is especially so when research is conducted using public funding (Wolfendale Committee 1995). Although recent trends such as public access policies (of both governments and granting institutions) and an increase in Open Access publishing mean that there is now improved access to scientific papers (Harnad *et al.* 2004, 2008), the challenge remains the engagement of people who do not consult such literature.

Work relating to how best to engage the public usually identifies barriers, such as a lack of communication skills, and solutions, such as increasing the school/university interface and personifying science using 'heroes' and examples from popular culture (Winter 2004). Work relating to the factors that motivate scientists to undertake such engagement (or not) are less predictable (Poliakoff & Webb 2007). However, it is important to note that there is reticence on the part of practitioners to actively engage. A study of almost 1500 scientists demonstrated that 64% believed their time was more appropriately spent on research, and – perhaps more importantly – 20% believed that engagement with lay people would result in a diminution of their reputation amongst peers (Royal Society 2006).

Given the vast array of media and communication options that are potentially available, it is also likely that in many instances scientists and/or their employing institutions may be overwhelmed by the very concept of attempting to determine which communication method or medium is most appropriate or accessible, and fearful that the risk of inaccurate reportage of research is a greater threat to their careers than the obscurity that results from non-engagement.

This case study is Australian and relates to the communication of an ecological project – as such the vast majority of sources are active participants within the fields of journalism and education rather than science. The immediate and obvious difference to traditional science is exemplified by this fact alone, for the reference list is dominated not by peer-reviewed papers but by radio, newspaper and internet articles. The need to accept such work as 'valid' or at least acceptable by scientists is fundamental to a better uptake of public engagement opportunities. However, evaluating the success of such public engagement endeavours is hampered by a lack of measurable indicators: in many instances the impact of a media story or education initiative can only be measured subjectively. Accepting this situation, or developing methods to evaluate initiatives such that they are recognized as part of what academics do, may be a necessary step in increasing participation.

Australia has several advantages as a country in which science communication – particularly biological science communication – could be better practiced, including a small, wealthy and technology savvy population, a single language, discrete borders and a unique assemblage of fauna and flora. However, few scientists are recognised by the general public outside their area of discipline. Notable exceptions include the paleontologist Professor Tim Flannery, well known as an author of natural history books and more recently as a spokesperson on climate science (Flannery 1994, 2005, 2012), the ecologist Professor Richard Kingsford, a vocal environmental spokesperson (Kingsford 2006) and the late Professor Peter Cullen, the founder of the Wentworth Group of Concerned Scientists. In all cases, the notoriety of these scientists outside academia has been facilitated by active engagement of media and communication opportunities and a willingness to partake in political and public debate (despite the hostility – up to and including death threats – that this occasionally engenders, R. Kingsford pers. comm).

This paper details the science communication work that has extended from 2009 to the present (2014) relating to a project that is attempting to prevent a small endangered fish, the red-finned blue-eye, *Scaturiginichthys vermeilipinnis,* from becoming extinct. Where possible, metrics (such as estimated audience, website visitation and monetary gifts) are used to demonstrate the success of the initiative. Other more subjective measures are also presented when they have been inferred and appear to be relevant. The project itself is summarised in the first section, followed by a description of the local/regional, national and international exposure that has been attained through science communication activities. In a separate but related section, the results of a survey of media and education professionals are summarised in order to support the project results and provide direct evidence of the requirements of these professionals regarding science communication material. In the conclusion, an appraisal of the communication efforts at all scales and the survey results are synthesized in order to make meaningful recommendations for the continuance and uptake of similar initiatives in Australia and elsewhere.

THE STORY – communication activities 2009–2014

The endangered red-finned blue-eye is a small (3 cm total length (TL)) fish that is only known from a group of Great Artesian Basin springs in semi-arid central-western Queensland (Figure 1). The property – Edgbaston – was purchased by the not-for-profit conservation organisation Bush Heritage Australia in 2008 with a view to conserving the spring complex and preventing red-finned blue-eye going extinct. The greatest threat to red-finned blue-eye is the invasive species eastern gambusia, *Gambusia holbrooki,* which is also present in the spring complex. All historical and anecdotal records indicate that invasion of individual springs by eastern gambusia results in red-finned blue-eye extinction (Fairfax *et al.* 2007), and when the property was purchased red-finned blue-eye were present in only four springs (Kerezsy & Fensham 2013). Recovery work commenced in 2009 with a view to determine control methods for eastern gambusia and establish populations of red-finned blue-eye in new and eastern gambusia-safe areas. More recently this work has included the construction of barriers around springs in order to prevent re-colonisation of red-finned blue-eye habitat by eastern gambusia during flooding, and in the future the establishment of a captive population is also planned. Most science communication work documented in the following sections relates directly to the project as whole

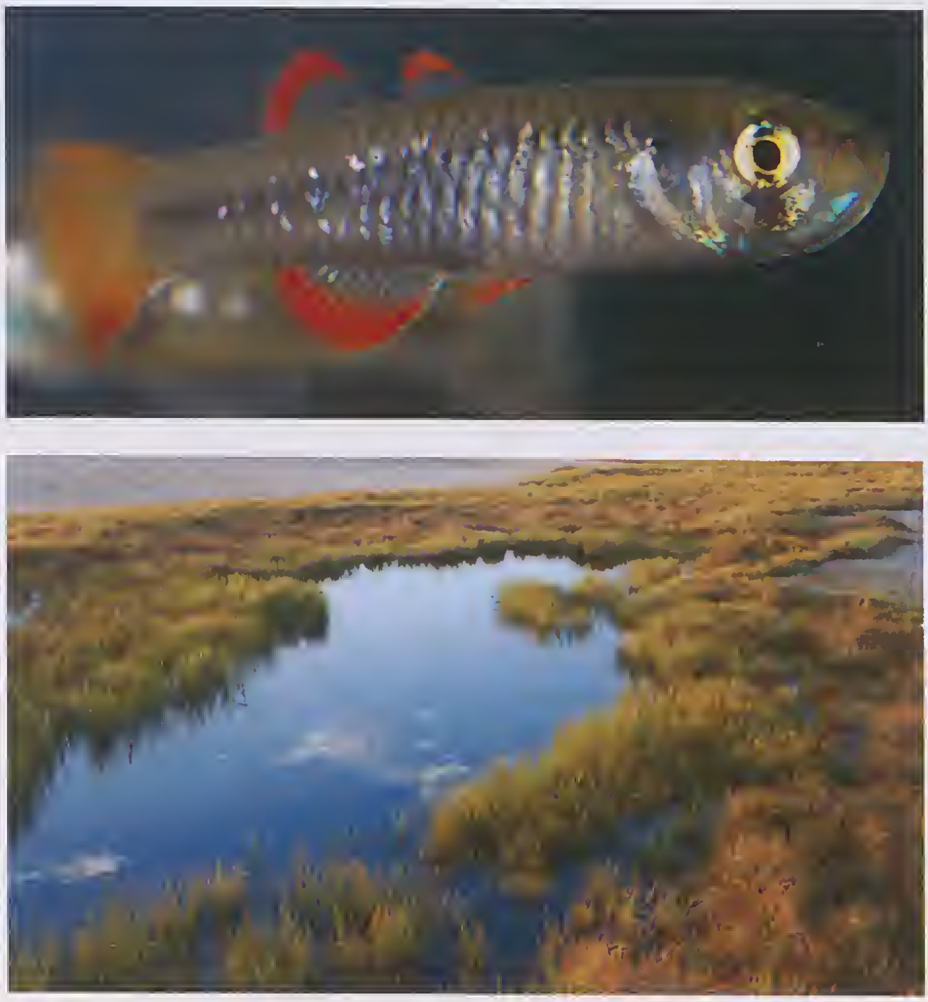

Figure 1 The endangered red-finned blue-eye from Edgbaston Reserve in central-western Queensland (above), and its habitat, a Great Artesian Basin spring (below) Photographs: Adam Kerezsy.

or specific aspects within it, and associated research is well represented and documented in the academic literature (Fairfax *et al.* 2007; Fensham *et al.* 2011; Kerezsy & Fensham 2013).

Local and regional science communication activities

The location of Edgbaston in central-western Queensland has facilitated continued access to the regional radio station (ABC Western Queensland) in Longreach, a small town that is a recognised transport, agriculture and services hub, and similarly easy access to the local newspaper, *The Longreach Leader*. In both instances, personal acquaintance with content managers and editors has meant that gaining access to these media organisations is as simple as a phone call, email or chance meeting. Between 2009 and 2014, approximately 20 radio interviews went to air (many also as internet stories) and five articles appeared in the newspaper (e.g. Clarke 2010; Harris 2011; Arthur 2012). All were either directly related to the project or addressed associated themes such as flooding and river health. It was particularly advantageous to be present in Longreach on many occasions and conduct interviews *in situ* at the radio station rather than over the phone.

The great advantage of radio in an isolated rural area is that there is only one radio station and that many landholders listen to the radio daily when going about their business. ABC Western Queensland has a potential listening audience of 57 000 (Nicole Bond pers. comm.) and covers the western half of the state of Queensland. Although it is difficult to judge the actual listening audience, anecdotal information suggests it is considerable: whenever a radio interview went to air, many acquaintances would relay the fact, and across a vast area of the country. A second advantage of radio, especially in isolated areas, is that scientific research is rare, and news and current affairs timeslots are often content-poor; presenters therefore welcome the opportunity to discuss local research. The red-finned blue-eye story offered (and continues to offer) a third advantage (which much research does not) as it is an on-going story and there are therefore numerous opportunities to present up-dates (for example post-flooding, post-storms and post-dry periods). Over time, the majority of the presenters at ABC Western Queensland have come to know the story themselves (as, presumably, have many listeners) and frequently begin an interview with a phrase like "So, how are the little fish going now?" This level of familiarity is a big advantage and means that presentation of up-dates has become more akin to a normal conversation than a formal interview.

In addition to local radio and newspaper stories, local coverage of the project was also achieved through public speaking at two conferences in western Queensland, the first in 2007 at the small town of Windorah (Kerezsy 2007) and the second in Longreach (Kerezsy 2013a). These presentations were advantageous more from a science communication than a pure science perspective because in both cases the audience was comprised of a combination of people with an interest in local land and water management including graziers, indigenous groups and townspeople. The Longreach conference provided the additional benefit of a video and internet record of each presentation, and this 20 minute talk was viewed 80 times in the 12 months since it was first posted (Kerezsy 2013b). A similar initiative by Desert Channels Queensland, the regional catchment management group, has produced a web-based video project (*Lake Eyre Basin: People and Passion* 2013) that presents interviews with a range of people with interest and expertise in various aspects of the area. At least four of the interviews have either a direct or indirect link to the red-finned blue-eye project and the springs at Edgbaston (Kerezsy 2013c; Silcock 2013; Fensham 2013; Tischler 2013) and the combined number of views for these presentations is currently 776 (as of March 30, 2014).

An additional advantage of the ABC radio interviews is that they are often syndicated throughout the organisation (which is national), and many have been reproduced at state (Queensland) and national level. Other media stories that reached a Queensland audience include several news stories in the daily newspaper *The Courier Mail* (Williams 2012; Edmistone 2012), a profile piece in *Q Magazine* (Bruce 2012) and a television current affairs segment that appeared on ABC television's *7.30* program (McLeish 2011a). Given the *Courier Mail's* circulation of 216, 638, the fact that *Q Magazine* is included in the Saturday edition and the nationwide reach of ABC television, it is likely that these pieces provided good statewide coverage of the project. It is noteworthy that in the vast majority of cases the thematic material in all media stories was very similar: a small and unusual fish, in a harsh and arid environment, with an enemy (eastern gambusia) and the efforts that were/are going towards saving it. Although science and experiments were/are occasionally mentioned, they have never been the focus of the reports.

In summary, the red-finned blue-eye project has received a substantial amount of media coverage at local, regional and state level. Any scientist conducting research in isolated or country areas of Australia could follow this example, and – most importantly – involve local people in their research through regular appearances on regional radio.

National science communication activities

There is a substantial difference between local/regional and even state communication activities and those at a national scale, and this is predominantly because the audience, though potentially much larger, can be assumed to have little idea of the context of the research (nor of the geography, climate and conditions in western Queensland in this particular case). This means that the story and main messages require further simplification and that there is usually a logistical component to the story (such as transporting and maintaining journalists in remote locations for several days). A potential advantage of this effort is that very often aspects of the transportation or maintenance can become part of the story themselves, and add to, rather than detract from, the central messages. A good example is the feature story that appeared in *Good Weekend* magazine (Bearup 2011), as wet conditions meant that the slightly dangerous drive out of the property was featured in the piece as well as the red-finned blue-eye story itself.

National news stories regarding red-finned blue-eye at Edgbaston have appeared in *The Age* (Smith 2012, circulation 197,500) and syndicated Fairfax newspapers (most notably the *Sydney Morning Herald*, circulation 207,013), on ABC Radio National and on the ABC's rural television flagship *Landline* (McLeish 2011b). The increasing trend of posting all stories on the internet (as well as in print media) is likely to mean that these figures are an underestimation of total audience reach. Additionally, many short news stories are often rendered in more detail as internet pieces: this was definitely the case with *The Age* story mentioned above, as the internet version included more photographs and a video interview. Given that this practice is likely to continue (Angela Wylie, Fairfax media, pers. comm.), it suggests that there may be multiple benefits of going to the trouble of transporting and maintaining journalists in remote areas for several days: the longer they are there, the more material they return with.

The benefit in terms of exposure of the project and attracting potential donors and supporters to Bush Heritage Australia (BHA) is difficult to judge in entirety but the metrics that are available are instructive (all following data courtesy of Bush Heritage Australia). Following publication of the *Good Weekend* feature article, unique visits to the BHA website increased by 300%, the number of pages visited doubled and an instant donation of $5000 was received. The equivalent value of the piece in terms of advertising space is estimated at $200 000. Following the airing of the story on *Landline*, three direct bequests were received by the company and website visitation increased to a similar degree. There was a 100% increase in website visitation following the news story published in *The Age*, where the equivalent advertising space rate is estimated to be $40 000.

Special interest magazines represent a different readership, often with prior knowledge of environmental

Figure 2 The full-page composite photograph that was used in the Good Weekend feature article (Bearup 2011; photography by Tim Bauer/Adam Kerezsy/*Good Weekend*).

and science issues but – again – limited knowledge of the project, the species or the area of interest. Their great advantage is that production values often result in the publishing of high quality images that can help to tell the story. The red-finned blue-eye story has been featured in magazines such as *Australian Geographic* (Pickrell 2012, circulation 82,339) and *Wildlife Australia* (Starbridge 2011). Like the more general news agencies, these magazines also present selected stories on the internet.

The success or failure of a feature article (in particular) often rests on the quality of the photographs rather than the story itself, and old adages (a picture tells a thousand words) appear to remain very applicable to modern media (Tim Bauer (freelance photographer), Angela Wylie (Fairfax photographer), Dean Caton (ABC cameraman), pers. comms.). The full-page picture that accompanied the *Good Weekend* feature is a good example: it encapsulated the Edgbaston story in one image by combining the fish, the landscape and the researcher (Fig. 2). This is especially significant given the readership of the magazine is 486,899 as it is an insert in both *The Age* and *The Sydney Morning Herald* – the largest newspapers in Australia's largest cities, Melbourne and Sydney, respectively – every Saturday.

The exponential growth of web-based media represents another way of publicising research, though the plethora of small sites and blogs can be difficult to negotiate. Red-finned blue-eye (and associated) pieces have been requested and published by sites such as *Realdirt.com* and *beforeitsgone.com* – both have a focus on environmental and/or wildlife related themes. A more high profile website with a science-focus is *The Conversation*, and profiles of both red-finned blue-eye and another endangered fish species, Edgbaston goby, *Chlamydogobius squamigenus*, have been published on this site as part of an on-going series concerned with Australia's endangered species (Kerezsy 2013d).

Gaining attention from non-science audiences can also be achieved by scientists publishing their work in different formats (ie: as opposed to peer-reviewed scientific literature). The natural history book *Desert Fishing Lessons* (Kerezsy 2011) is a relevant example, though there are many others (Johnson 2006; Pepperell 2010). Though not specifically concerned with the red-finned blue-eye story, the book touches on it, but perhaps more crucially enabled national coverage through a range of print media (particularly reviews) and an hour-long radio interview on the ABC's *Conversation Hour* program (Dalton 2011). An interview of this length is unprecedented in most other forms of media in Australia and represents a unique vehicle for communicating research to a very wide audience. More specific – and far more politically-aligned – is the periodical *Quarterly Review*. Being invited to respond or contribute to such a publication (Flannery 2012; Kerezsy 2013e), presents different opportunities: in this case to discuss political aspects of the Edgbaston story, most particularly the weaknesses of the existing regulatory framework concerning endangered species management in Australia.

Last, a substantial amount of public speaking also characterised the national communication events from 2009–2014. A total of 26 conference and similar presentations occurred, and although the majority were to science audiences at conferences such as Australian Society for Fish Biology, Australian Society for Limnology, Ecological Society of Australia and the Australasian Wildlife Management Society (e.g. Kerezsy 2009; 2010), notable exceptions included presentations to fish hobbyists through the Australia and New Guinea Fish Association (ANGFA), to a variety of community organisations and school groups and to a general audience at the Wheeler Centre in Melbourne, a talk that is also published online (Kerezsy 2012a).

A national approach to science and research communication does not have the intimacy of local and regional work, but this is balanced by the far higher potential audience and the flow-on effects that can occur. Communicating at this level is vital if organisations with a national reach (such as Bush Heritage Australia) wish to engage the general public in the conservation work they are undertaking and, by association, attract more donors and active supporters. Feature articles in weekend newspaper magazines are a traditional and obvious goal if such coverage is desired, however this may change as print media increasingly turns to online delivery of content.

International science communication activities

The rationale for making an effort to communicate aspects of the red-finned blue-eye project outside the academic literature stems from interest from international aquarists and fisheries ecologists in the papers that have been published thus far, combined with the demonstrated ease with which the species and the story effectively 'sells itself'. To be accurate, however, coincidence and opportunism could equally be appropriated: once a story such as this is available worldwide via the internet the material is effectively already 'international', and extra opportunities can be selected on merit.

The fish and its story has certainly been featured in German literature (Godlinski 2014), and interviews granted in an effort to convey the story as truthfully as possible across the language divide. However, the most high-profile international exposure that the project has received to-date has been inclusion in the IUCN's Breaking Point initiative, which aimed to highlight the plight of the 100 most endangered species worldwide (Kerezsy 2012b).

Although communication of most local research at international level is probably not necessary, desirable or possible, in instances where the subject has international appeal it should be considered, because even if the international exposure does not generate further international support or interest, its very existence is likely to elevate the profile of the work locally and nationally. In the case of the red-finned blue-eye, being listed as one of the most endangered species in the world (along with high profile terrestrial animals like the Javan and Sumatran rhinoceros) has elevated the status of a small colourful desert fish to a flagship species for the springs in which it lives, the harsh-yet-fragile Australian interior and the organisation that is sponsoring its recovery.

Table 1 Participants in the survey of media professionals who provided responses to the questions.

Name	Position/occupation and location
John Pickrell	Editor, *Australian Geographic* magazine, Sydney, NSW
Alun Hoggett	Digital Productions Consultant, Desert Channels Productions, Longreach, Qld
Terri-Ann White	Director, University of Western Australia Publishing, Perth, WA
Darren Shepherd	Principal, Toohey Forest Environmental Education Centre, Brisbane, Qld
Nicole Bond	Regional Contact Manager, ABC Western Queensland, Longreach, Qld
James Whitmore	Deputy Section Editor, Environment + Energy, *The Conversation*, Sydney, NSW
Kathy McLeish	ABC journalist, *7.30 Qld* and *Landline*, Brisbane, Qld
Brian Williams	Environment reporter, *Courier Mail* newspaper, Brisbane, Qld
Michelle Ransom-Hughes	Producer, *Conversations with Richard Fidler*, ABC, Brisbane, Qld
Chris Feik	Editor, Black Inc. books, Melbourne, Vic

THE SURVEY – what the media want

Three survey questions were emailed to a list of professionals working across a range of media (print, radio, television, magazine publishing, book publishing and internet) and at the same local/regional and national scales mentioned previously in the text (Table 1). The aim of the survey was encapsulated in the following questions and it was designed to allow participants to spend a minimum of time on the exercise (while still harvesting useful information):

1. What makes a science story easy or laborious?
2. What could researchers do better?
3. Any other large or small piece of advice that you think may be useful to scientists.

Responses to the survey were categorised based on the information that was returned (Fig. 3). The highest priority amongst all media professionals (70% of all responders) was the requirement for researchers to be able to make their work relevant to the everyday lives of potential audiences and to be able to enunciate why their research is important, and the second highest priority (60%) was the need to use simple language or prose and a minimum of scientific jargon. Two responders used the analogy of explaining research at a level that would be understandable by a grandparent (Nicole Bond, ABC, and John Pickrell, *Australian Geographic*). The ability to tell a story was identified by 30% of the responders as important to good science communication, and the need to imbue the story with either drama or humour and the inclusion of good visual material (either photographs or video) was important to 20% (Fig. 3).

Although the majority of responses to the questions had common themes and could be easily categorised (Fig. 3), some items of extra advice could not. Among these, one of the most useful is that scientists that demonstrably lack communication skills may be better off entrusting the communication of their work – no matter how interesting – to a third party such as a colleague or friend, the implication being that no matter how skilled or talented a scientist may be, some may not be able to master the communication skills required (Terri-Ann White, UWAP). Although this has similarities to the more formal concept of a science communicator or knowledge broker (Meyer 2010), it is more intimate and suggests that within a collegiate group of science professionals the individuals with the most advanced communication skills should – perhaps – be identified and permitted to represent the work of others in communication activities.

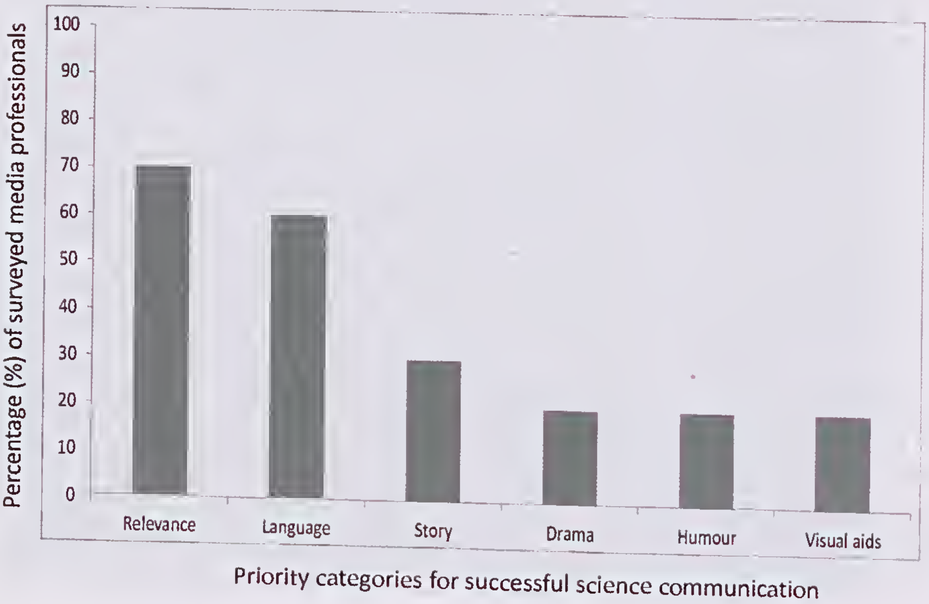

Figure 3 A graph showing priority categories identified by Australian media professionals for successful communication of scientific research projects to a wider audience.

CONCLUSION

The case study presented in this paper and the survey of media professionals who work in science communication are instructive in terms of planning and implementing science communication activities with the aim of raising the profile of a particular project or initiative. The red-finned blue-eye project at Edgbaston has several advantages when evaluated against the priorities of the media professionals. It has always been communicated with simple language, possibly because the initial communication activities (through ABC local radio) aimed to explain the project to a local and regional audience who, though familiar with the landscape, were not generally familiar with science or research. A great deal of effort went in to the 'relevance' aspect of this communication work, and the project was made relevant because a) the fish was endangered and close to extinction and b) the fish happened to inhabit an isolated and unusual part of Australia. In this way, local and regional people have come to have some ownership or interest in the project, despite not necessarily being intrinsically interested in fish or springs to begin with (Michael Wills (Barcaldine), David Coulton (Aramac), Jason Dollinger (Ilfracombe), pers. comms).

The red-finned blue-eye project has always been presented as an on-going story: the various chapters have included all aspects of the project to-date including experiments to try and control the invasive species eastern gambusia, the legislative issues surrounding working on endangered species, the success and failure of red-finned blue-eye relocation events and the effects of droughts or floods. It is notable that exactly the same information has been presented in peer-reviewed papers, though in a far different form (Fensham *et al.* 2011; Kerezsy & Fensham 2013). Dramatic and humorous events have peppered the popular literature and media stories, no doubt adding to their appeal (Bearup 2011; McLeish 2011a; Smith 2012), and this is the major difference between the scientific and other reportage. For better or worse, there is no place for such digression in peer-reviewed science. Last, Edgbaston – the property, its harsh and almost-lunar landscape – and the fish itself, have provided ideal visual accompaniment to the large body of written work that has been produced.

The science communication effort that has gone into Edgbaston and saving the red-finned blue-eye has been productive for the sponsoring organisation, and has elevated public knowledge of the species and its plight. Although it remains difficult to evaluate the degree to which this has occurred, enough subjective evidence exists to conclude that there is far more reason to communicate such projects to a wider audience than to refrain from doing so.

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In memory of Michael Wills from Edgbaston, 1966 – 2014.

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Emergence of field-based underwater video for understanding the ecology of freshwater fishes and crustaceans in Australia

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Underwater video is increasingly being used to record and research aquatic fauna in their natural environment, and is emerging alongside Dual Frequency Identification Sonar (DIDSON) as a powerful tool in Australian freshwater ecology. We review current progress with field-based applications of underwater video in studying Australian freshwater fish and crustacean ecology. Drawing upon searches of online literature databases and our expert knowledge, we located 11 relevant publications: five set in the Murray-Darling Basin, three in the Eastern Province, two in the Northern Province and a single study in the Pilbara Province. In total, 10 studies reported using video for fish ecology, while three studies included crustaceans. Across the 11 publications, eight examined threatened species, while the remaining studies developed video techniques for surveying species richness in remote or difficult to access habitats. Habitat-use was also a dominant theme (seven studies). Seven of the eight studies that centred on threatened species focused on at least one percichthyid species in either the Murray-Darling Basin or the Eastern Province. Miniaturisation in equipment and increases in compact battery capacity seem to have driven a shift from above-water battery supplies and data storage to small, inexpensive and mobile underwater cameras. We foresee wider use of video in freshwater ecology primarily in the study of animal behaviour and also to improve species detection in field surveys. There is scope for testing novel techniques such as animal-borne video and unmanned underwater vehicles and making use of video in citizen science initiatives.

KEYWORDS: freshwater ecosystems, review, visual survey methods, aquatic fauna, animal behaviour, bait

INTRODUCTION

Underwater video, operated either manually or remotely, has been readily adopted in marine habitats spanning complex shallow reef biomes (e.g. Harvey *et al.* 2007; Holmes *et al.* 2013) to deep waters (e.g. Priede & Merrett 1996). Although less prevalent, video has also been used to research freshwater fauna in both laboratory (e.g. Lamprecht & Rebhan 1997) and field settings (e.g. Hinch & Collins 1991; Weyl *et al.* 2013). Such video applications have enhanced our understanding of the behaviour and physiology of Australian freshwater taxa, particularly with regard to captive individuals in laboratory settings (e.g. Richards & Bull 1990; Brown 2001; Crossland 2001; Karplus *et al.* 2003; Lowry *et al.* 2005; Wilson 2005; Patullo *et al.* 2007; Svensson *et al.* 2012). Areas of study have included turtle diving experiments (Priest & Franklin 2002; Clark *et al.* 2009), feeding, swimming and reproductive behaviour of the platypus, *Ornithorhynchus anatinus* Blumenbach, 1800 (Hawkins & Fanning 1992; Evans *et al.* 1994; Manger & Pettigrew 1995; Fish *et al.* 1997, 2001; Hawkins 1998; Holland & Jackson 2002; Hawkins & Battaglia 2009), and interactions involving amphibians including the alien cane toad, *Rhinella marina* (Linnaeus 1758) and its tadpole phase (Crossland 2001; Squires *et al.* 2008; Hamer *et al.* 2011; see also Shine 2014 and references within).

Field applications of video in Australian freshwaters have involved both above-water and underwater filming, such as the behavioural studies of waterbirds (e.g.

Dorfman *et al.* 2001; Murray & Shaw 2009; Winning & Murray 1997), crocodiles (Fig. 1e; Doody *et al.* 2007; Steer & Doody 2009; Somaweera & Shine 2011; Somaweera *et al.* 2011) and frogs (Byrne & Roberts 2004). In recent years, however, underwater video studies have been increasingly common. These studies have focussed on both fishes and crayfishes, and have often targeted clear-water systems (e.g. Butler & Rowland 2009), although some turbid-water examples exist (e.g. Fulton *et al.* 2012). Rapid advances in digital camera technology and affordability have likely driven this expansion.

While video has progressed our ecological knowledge, we believe the full potential of this technique is yet to be realised. Video is likely to be most helpful in understanding the ecology of speciose groups of large-bodied fauna, such as freshwater fishes, crayfish and large-bodied palaemonids (prawns of genus *Macrobrachium*) (Short 2004; Crandall & Buhay 2008; Humphries & Walker 2013) in difficult to access aquatic habitats. Here we aim to: i) review field applications of underwater video in studying freshwater fishes and crustaceans in Australia, ii) draw upon the collective experiences of researchers to identify advantages and disadvantages of video-based methods, and iii) outline future avenues for video to provide fundamental insights into freshwater ecology, particularly in an Australian context.

Field applications in Australia

Literature searches were conducted in three online databases (Web of Science, Scopus, National Library of Australia (NLA)) to identify relevant primary and grey literature. A single composite search term was used to identify literature that employed video or camera-based systems within Australian freshwater ecosystems: (video OR camera OR film OR visual) AND (freshwater OR aquatic OR river OR lake OR billabong) AND Austral*). The Web of Science search was restricted to 'Topic' and articles in English. Likewise, the search in Scopus was restricted to article "Title, Abstract and Key Words". The search in the NLA database was open to all fields (title, subject, author, publisher, series, ISBN/ISSN/ISMN, occupation), but restricted to books, newspapers, journals and manuscripts. Searches were not restricted to specific time periods, for example the Web of Science database searched from 1945–2014. Searches were performed in all three databases on 17 June 2014, and literature examined for relevant articles that examined aquatic fauna using camera systems in the field. Each article was evaluated based on its title and excluded if clearly not relevant (e.g. not on Australian ecosystems or not of biological or ecological context). Abstracts were examined for relevant papers (i.e. studies in Australian freshwater ecosystems with a biological context). Articles that did not identify the application of video systems were excluded.

Searches returned an initial total of 170, 190 and 209 articles from Web of Science, Scopus, and the National Library of Australia (NLA) databases, respectively. Further reading of these revealed six relevant journal publications identified in Web of Science, and no additional relevant literature was discovered via Scopus nor the NLA. A survey of Australian freshwater fish researchers (our authorship team) identified five additional publications. These publications included a recently accepted paper on the *Marine and Freshwater Research* website, an honours thesis, a report chapter and two government reports. The earliest of all these relevant publications was published in 2006.

Publications describing field-based applications of video were then coded according to five attributes: a) the freshwater fish biogeographic province (according to Unmack 2013) where the study was undertaken, b) focal taxa (fish, crustacean, other) and whether they were conservation listed species (Federally; and if not State listing was checked), c) primary study aims relevant to video application, d) type of camera equipment, and e) camera submergence (above water only, underwater only, both above and below water cameras). If details were ambiguous, we directly corresponded with the lead author to obtain the relevant information.

Location and focus of studies

Each study was set within a single bioregion; five were based in the Murray-Darling Basin (see Figure 1a, d), three in the Eastern Province, two in the Northern Province (see Figure 1b) and a single study in the Pilbara Province (Table 1). All studies except one reported filming fishes (e.g. Figure 1c), and three studies examined crustaceans (Figure 1d) (Table 1). Eight studies were oriented towards threatened species and the remaining three were focussed on developing video survey techniques for estimating species richness in remote or difficult to access habitats (Table 1). Seven of the eight studies that explored threatened species focussed on at least one percichthyid in either the Murray-Darling Basin or the Eastern Province (Table 1).

Habitat-use was a common theme, with seven studies exploring patterns of habitat occupation through time and/or space (including foraging, Table 1). These studies had a variety of aims (Table 1): four investigated reproduction, by filming spawning sites and/or parental care (Butler & Rowland 2009; Tonkin *et al.* 2009, 2010; Butler *et al.* 2014); two investigated depth occupation by fishes (Cousins 2011; Ebner & Morgan 2013); and one examined use of artificial habitat (Lintermans *et al.* 2010). Two publications reported using video techniques in concert with radio-tracking to determine habitat-use (Butler & Rowland 2009; Lintermans *et al.* 2010).

Examining the efficacy of survey methods was another key objective. Three studies compared video to other survey techniques (Fulton *et al.* 2012; Ebner *et al.* 2014) and one of these and an additional study compared baited and un-baited cameras (Ebner & Morgan 2013; Cousins 2011). Three studies compared estimates of species richness, principally of fish assemblages but also crustaceans (crayfish and palaemonids) and turtles (Cousins 2011; Ebner & Morgan 2013; Ebner *et al.* 2014). Additionally, Fulton *et al.* (2012) compared the efficacy of video, manual snorkel surveys and capture-based techniques for estimating the density and abundance of a crayfish species. While some video studies of fishes also observed turtles, mammals or birds, this was not necessarily part of their explicit aims (e.g. Butler & Rowland 2009; Lintermans *et al.* 2010).

A number of studies investigated video post-processing efficiencies (Ebner *et al.* 2009; Lintermans *et al.* 2010; Cousins 2011; Ebner & Morgan 2013). These

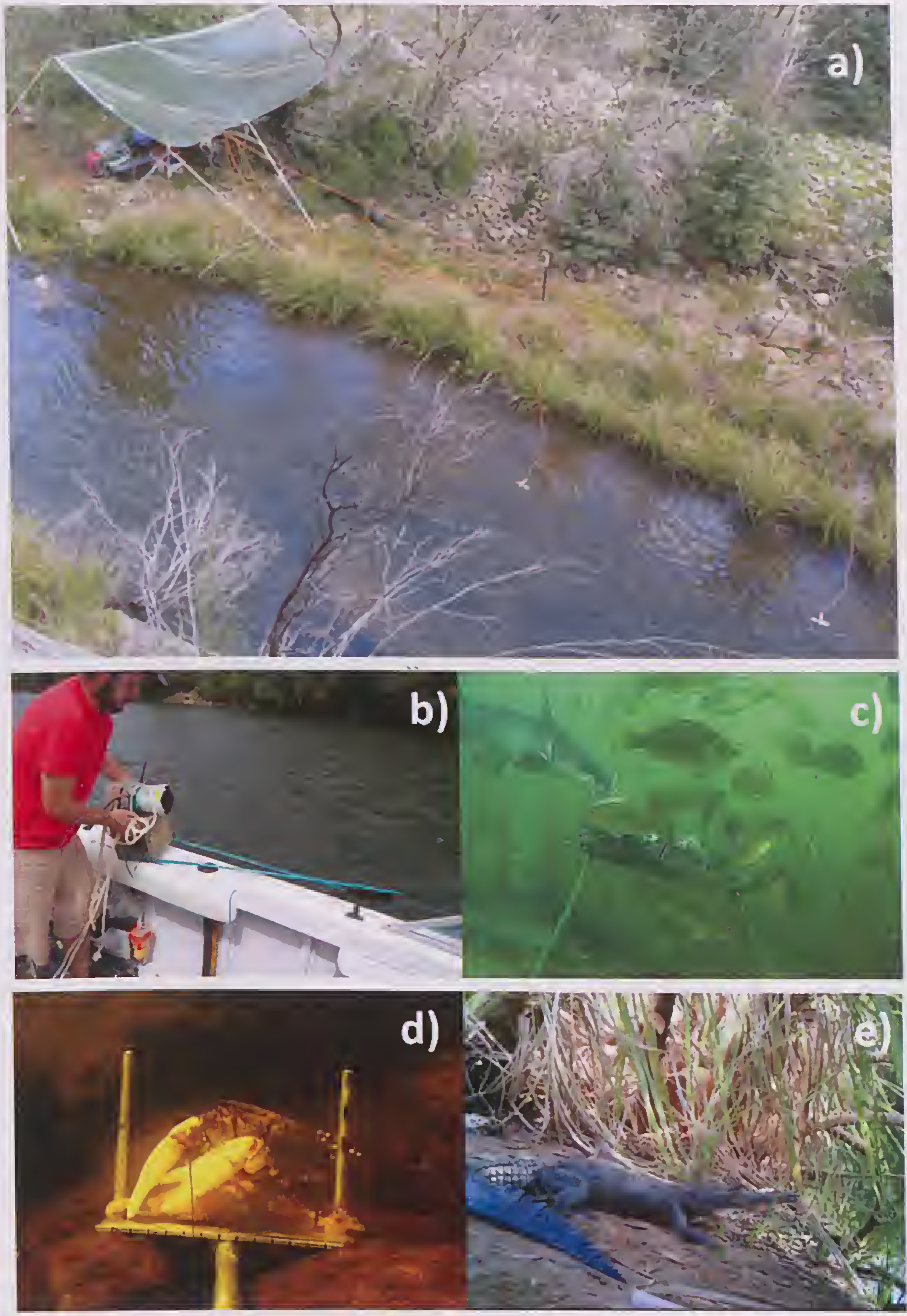

Figure 1 Field based studies of Australian freshwater fish and crustaceans began with a) the use of underwater cameras tethered to shore-based video cassette recorders and multiplexor units powered by a large battery supply (under tarpaulin), and has more recently expanded to include use of self-contained camera systems for b) deployment of baited camera, c) surveying fish assemblages, and d) counting crayfish; whereas, e) above water cameras have generally been used to study the behaviour of semi-aquatic fauna including freshwater crocodiles.

Table 1 Summary of field-based video studies of freshwater fishes and crustaceans in Australia to date. Biogeographic province was based on Unmack (2013) and conservation status was based on EPBC listing else state-level listing if not federally listed.

Study	Biogeographic province	Focal species	Conservation status	Focal taxa	Study aims	Camera equipment	Artificial lighting	Camera location
Broadhurst *et al.* 2006	Murray-Darling	*Maccullochella macquariensis*	Endangered	Fishes	Threatened species; behaviour; species reintroduction	Bankside VCR & Multiplexor & LCD screen (Analogue)	No	Above and below water
Butler & Rowland 2009	Eastern	*Maccullochella ikei*	Endangered	Fishes	Threatened species; behaviour; reproduction/ spawning habitat-use; overall habitat-use	Bankside VCR & Multiplexor & LCD screen (Analogue)	Yes	Below water
Ebner *et al.* 2009	Murray-Darling	*Macquaria australasica, Gadopsis bispinosus*	Endangered (*M. australasica*), *G. bispinosus* vulnerable in ACT	Fishes, crustaceans	Threatened species; behaviour; diel activity (including nocturnal)	Bankside VCR & Multiplexor & LCD screen (Analogue)	Yes	Below water
Tonkin *et al.* 2009	Murray-Darling	*Macquaria australasica*	Endangered	Fishes	Threatened species; behaviour	Bankside Computer & monitor (Digital)	No	Below water
Tonkin *et al.* 2010	Murray-Darling	*Macquaria australasica*	Endangered	Fishes	Threatened species; behaviour; reproduction spawning habitat-use; overall habitat-use	Bankside Computer & monitor (Digital)	No	Below water
Lintermans *et al.* 2010	Murray-Darling	*Macquaria australasica*	Endangered	Fishes, mammals, birds, crustaceans	Threatened species; behaviour; water resource management; artificial habitat-use; overall habitat-use	Bankside personal video recorders (PVR) (Digital)	No	Below water
Cousins 2011	Northern	Fish assemblage level	N/A	Fishes	Depth-use; overall habitat-use; species richness; technique comparison	Submerged Handycam (Digital)	No	Below water
Fulton *et al.* 2012	Murray-Darling	*Euastacus armatus*	Vulnerable (ACT) Vulnerable (NSW)	Crustaceans	Threatened species; behaviour; abundance assessment; technique comparison	Submerged Handycam (Digital)	No	Below water
Ebner & Morgan 2013	Pilbara	Fish assemblage level	N/A	Fishes	Depth-use; overall habitat-use; species richness; technique comparison	Submerged Handycam (Digital)	No	Below water
Ebner *et al.* 2014	Northern	Freshwater fauna	N/A	Fishes, reptiles, crustaceans	Species richness; technique comparison	Submerged Handycam (Digital)	No	Below water
Butler *et al.* 2014	Eastern	*Maccullochella ikei*	Endangered	Fishes	Threatened species; behaviour	Boat-mounted VCR & Multiplexor & LCD screen (Analogue)	Yes	Below water

included investigations of sub-sampling strategies relating to the amount of video processed, and in some cases the speed at which video could be manually processed to extract certain types of data.

A diverse spread of other topics was encompassed within this underwater video literature, including: elements of threatened species reintroduction (Broadhurst *et al*. 2006), angler effects on a threatened species (Butler & Rowland 2009), diel activity of crustaceans and threatened fishes (Ebner *et al*. 2009).

Video equipment

Three main types of equipment configurations were used in the studies we reviewed: a) bank-mounted video cassette recorder and tethered monochrome cameras, b) underwater digital cameras with tethered data storage units, and c) portable digital cameras with self-contained small rechargeable lithium batteries. Some of the first video-based studies used monochrome cameras (suited to low light conditions) tethered to bank-side (Broadhurst *et al*. 2006; Butler *et al*. 2009; Ebner *et al*. 2009) (Figure 1a) or boat-mounted (Butler *et al*. 2014) video cassette recorders (analogue) equipped with LCD screens or connected to laptop computers and powered by large batteries (traditional or gel cell lead acid batteries). These studies often used multiplexors to divide recorded frames from multiple cameras, and mostly relied on underwater filming. Broadhurst *et al*. (2006) was an exception in using both above and below water cameras. Artificial lighting was used in the studies of Butler & Rowland (2009) and Ebner *et al*. (2009).

The second type of video equipment was used in a single study involving underwater digital cameras with tethered data storage units and large batteries positioned on shore (Lintermans *et al*. 2010). This involved programmed personal video recorders (PVRs) that facilitated long term surveillance (days to weeks) without requiring manual intervention to change video cassettes. However, periodic downloading of video data was undertaken to minimise the risk of losing data. No artificial lighting was used.

More recently, the third type of equipment in the form of portable digital cameras with self-contained small lithium batteries has been adopted, which removes the need for onshore tethering to a power supply or recording device, but this can limit the filming duration (typically < 3 hrs). To date these applications have been confined to underwater day time filming in colour in the absence of artificial lighting (e.g. Cousins 2011; Fulton *et al*. 2012).

ADVANTAGES, DISADVANTAGES & CHALLENGES

Advantages

There are a number of advantages with using underwater video-based research to monitor freshwater fauna. It may represent the only viable or safe technique for answering particular types of research questions in certain environmental settings (e.g. Ebner & Morgan 2013; Ebner *et al*. 2014). For instance, video surveillance provides researchers with unparalleled opportunities to observe and measure behaviour (e.g. aggressive interactions, spawning activity and feeding mechanisms) otherwise unmeasurable by conventional survey techniques. Furthermore, video provides opportunity for long-term monitoring of behaviour where a human observer would become fatigued or would be in danger, as in many crocodile-inhabited tropical systems, or where the presence of researchers represents an unacceptable intrusion on aquatic community behaviour (e.g. Butler & Rowland 2009; Ebner *et al*. 2009, 2014). Similarly, underwater cameras may be useful for studying ecology in wetlands where access is difficult or is highly restricted, such as on military bases or airports. Cameras also permit observation in areas too deep (Cousins 2011) or fast-flowing for alternative sampling equipment, or in areas too shallow or complex for diver access (notwithstanding logistical issues). Video applications may also be highly desirable for discrete studies in environmentally sensitive areas. Examples include where humans demand a high standard of water quality (e.g. drinking water supply catchments, small springs) or where aesthetics and social considerations are paramount (e.g. urban parks, certain tourist viewpoints, national parks).

The non-destructive aspect of visual surveys, including video, is also ideal for studying rare or threatened species that are stressed, harmed or killed by capture-based methods and associated handling. For instance, amongst Australian freshwater fishes, clupeids, retropinnids and certain atherinids are sensitive to net abrasion, and electrofishing of *Maccullochella* and certain gudgeons (e.g. *Eleotris fusca*) requires special care. Moreover, even for species for which capture and handling is non-lethal or not obviously harmful, there is an ethical consideration around the trade-off between increasing data collection and increasing system disturbance. This consideration is perhaps most obvious in small systems where researcher disturbance modifies benthic habitat, temporarily impacts water clarity and may impact sensitive riparian vegetation.

Video also provides a record that can be reassessed in the future. With appropriate provisions for storage and future video file compatibility, footage can be reanalysed in the pursuit of new lines of enquiry, enabling virtual field trips back in time. Data extracted from the video can be checked or modified, perhaps with more advanced analytical techniques. Considering the cost of field trips to remote locations, being able to mine film archives of permanent records of underwater environments and faunal communities seems likely to benefit ecologists that specialise in particular fauna groups, even if those species were not initially targeted. Video replay also enables the slowing of frame rates to enable measurement of behaviour that would otherwise be impossible for the human eye to resolve (e.g. Breder & Edgerton 1942).

Video clearly has a role to play in public communication. Mainstream documentaries that engage and educate the public about the natural world are immensely popular. In this regard, researchers have much to gain from using their underwater films to entertain and educate non-researchers about new discoveries. This can be done via freely available public online video resources (e.g. YouTube, Vimeo). Arguably, few other survey techniques used to study freshwater fish and crustaceans have this capability of reaching broad audiences and large numbers of people around the globe. The potential to showcase our unique Australian freshwater fauna is large. For example, during an 18 month period, over 3,000 people viewed YouTube footage of Murray crayfish collected by Fulton *et al.* (2012).

Disadvantages

A primary limitation of visual survey techniques involving video is their reliance on clear water, and therefore, poor function in turbid waters (Broadhurst *et al.* 2006). This means that video has limited applicability in many of the large lowland rivers of northern and inland Australia, such as Cooper Creek and the Darling River (e.g. Fellows *et al.* 2009), or tannin-stained swamps and wetlands. Systems exposed to severe or common sediment disturbance may also render themselves inappropriate for video research. For instance, a major bushfire in the Australian Capital Territory led to sedimentation of local streams which thwarted a short-term video-based research project (Ebner *et al.* 2009) and stifled a separate research project years later when re-suspension of sediment following a major rainfall event coincided with a translocation experiment (Broadhurst *et al.* 2006). Furthermore, our collective experiences include a number of unpublished field exercises where video was severely compromised by temporarily elevated turbidity associated with short-term high rainfall and sediment run-off events. However, in some cases it may be possible to use video in turbid waters, such as the study by Fulton *et al.* (2012) which was able to exploit the attraction of Murray River crayfish to bait to capture their presence in the Cotter River. Dual Frequency Identification Sonar (DIDSON) (Tušer *et al.* 2014) provides a promising alternative to video-based techniques in turbid environments.

Another disadvantage is light limitation. The dependence of cameras on light means that studies are typically confined to daylight hours. This means that species particularly active at night, such as some freshwater catfishes, may be underestimated by video. Two studies have used video at night: a pilot study monitoring the diel activity of threatened fishes in the Cotter River based on infrared lighting (i.e. Ebner *et al.* 2009) and a study recording the diel behaviour of nesting Eastern freshwater cod (*Maccullochella ikei* Rowland 1986) based on white lighting (Butler & Rowland 2009). Whilst infrared lighting is likely to be important for non-obtrusive behavioural studies, the use of conventional lighting and baited cameras may be a viable option for detecting the full breadth of nocturnal fauna diversity; and in fact light may serve as an additional attractant for certain taxa.

Hardware malfunction or poor performance of cameras can also be an issue. Electrical errors can occur when collecting and storing video, batteries can overheat or degenerate, and memory media can become corrupted (Lintermans *et al.* 2010; Ebner *et al.* 2014). Camera performance declines when lenses are fogged or when glare or reflection is intense. Fogging can be countered with desiccant bags and glare and reflection can be partially dealt with by carefully positioning cameras relative to the position of the sun and by using lens filters.

Another important limitation of underwater video is reduced confidence in taxonomic identification. This is especially relevant when viewing small individuals, those that are distant from the lens, or for species that do not have easily distinguishable morphological or behavioural traits. For example, Lowry *et al.* (2011) noted difficulty in discerning fish species with similar appearance (typically juveniles) or those that move rapidly past the camera. These factors are unlikely to be an issue for Australian crayfish because individuals move slowly and species richness is usually low within any catchment or site. However, the identification of small-bodied species, including the early life history phases of many fishes, is likely to be a real difficulty at sites with high species richness and multiple small-bodied species. This is probably more of an issue in the tropics, but may also be an issue at specific locations in temperate Australia where sympatry of congeneric species occurs [e.g., where multiple *Nannoperca* spp. cohabit in south Western Australia (Morgan *et al.* 2013) and south eastern Australia (Saddlier *et al.* 2013), and where galaxiid species richness is high (Adams *et al.* 2014)]. However, in some fish assemblages, such as where sicydiine gobies are a feature of short-steep-coastal streams in the Wet Tropics, there are times of year when heightened coloration aids the video-based demarcation of sympatric congeneric species (and sexes) during extended courtship periods (Ebner & Donaldson, pers. obs.).

Methodological challenges

An important issue in the emerging field of freshwater video research is differential detection associated with different types of bait (including no bait), different baiting methods, and different environmental conditions. This variation in detection capability reduces our ability to compare the findings within a study through time and space, to compare between different studies and to conduct meta-analyses.

Different baits and baiting methods have arisen because researchers target different species or taxa (e.g. fish versus crayfish), or because sometimes they target single species and at other times the assemblage (e.g. threatened species versus whole fish community). We currently know little about the ability of different baits to attract freshwater taxa, but we know that some species prefer one bait type over another and that the freshness of bait is likely an important factor (Løkkeborg & Johanessen 1992; Dorman *et al.* 2012). We also know the capacity of bait to attract species will differ depending on whether or not a species primarily hunts visually or by olfaction (Bassett & Montgomery 2011).

One approach to control for detection is to standardise bait type and baiting method. Considerable efforts have been made to find a suitable standard bait. For example, many of the authors of this paper have investigated the use of defrosted pilchards, *Sardinops sagax* (Jenyns 1842) – a bait that is widespread in marine video studies (e.g. Harvey *et al.* 2007; Holmes *et al.* 2013). Unfortunately, field trials by the authors of the current paper have revealed practical considerations that need to be resolved for this bait type to be successful. Issues include the limited refrigerated storage space in cars, boats, helicopters or on-person, and the poor longevity of bait during long and remote field trips (greater than a week). We encourage more pilot studies that investigate optimal baits for species or assemblages.

An alternative to standardising bait is to use un-baited cameras. There is currently much contention about whether or not to bait. A small amount of defrosted bait or canned food may draw certain rarely-detected species to the camera thus saving post-processing time and effort, but deploying more replicates of un-baited cameras requires less hassles with field equipment (e.g. bait bags and associated mounting structures) and bait storage requirements, improving portability and accessibility in remote areas. Comparisons of baited and un-baited cameras in Australian freshwater systems have revealed subtle differences in species richness estimates derived by either technique (Cousins 2011; Ebner & Morgan 2013). Preliminary indications are that camera placement with respect to depth and microhabitat may actually be more influential for estimating species richness and assemblage composition in freshwater systems than baiting or not baiting cameras (Cousins 2011; Ebner & Morgan 2013; Ebner *et al.* 2014). Unfortunately, overcoming some of these issues is not as straightforward as increasing the numbers of camera placements. Pseudo-replication and double-counting of individuals come into consideration. In the case of baited cameras, how bait type affects species detection and species selectivity remains to be investigated in freshwater systems. This extends to understanding how fish assemblages behave in relation to the activity of a subset of species that is stimulated by introducing a bait.

An alternative and more sophisticated approach is to use mathematical models such as Bayesian hierarchical models (Royle & Dorazio 2008) that estimate and correct for variation in detection (e.g. Beesley *et al.* 2014). These models use variation in data among replicate cameras to estimate detection at the site level, and then correct estimates of abundance (or occupancy) for differences in detection among sites. Picture frames from a single camera may also be treated as replicates, allowing variation in detection through time to be modelled (see Coggins *et al.* 2014). This will allow data that have been collected from cameras with different deployment times to be legitimately compared. The models are fairly robust but inference can be further strengthened by collecting information on the variables likely to affect detection. We recommend that researchers collect information relating to variables that describe bait-attractiveness and effectiveness (e.g. bait type, bait size, water depth or volume, and flow velocity), and those related to camera efficiency (camera type, water turbidity, light levels, camera depth in water, surrounding habitat etc.).

FUTURE APPLICATIONS

Most published field-based applications of video research of Australian freshwater fishes and crustaceans have centred on threatened species (particularly percichthyids). In many cases, these studies have employed video to understand behaviour and habitat use. The discovery that *M. ikei* parentally guards its egg and larvae (Butler & Rowland 2009) is a clear demonstration of the type of ecological information that can be obtained by underwater video that is unattainable by conventional methods. From an applied perspective, an application of underwater video surveillance to test *Macquaria australasica* Cuvier, 1830 association with particular artificial habitat (Lintermans *et al.* 2010) was invaluable in attempting a level of sustainability for a major dam construction project in the Australian Capital Territory. Both of these examples used video to complement applications of radio-telemetry and deployed multiple cameras over multiple seasons or years (Butler & Rowland 2009; Lintermans *et al.* 2010). Together these studies indicate the benefits of video for threatened species research, alongside the tremendous scope for using highlights from research footage to promote public interest and increase understanding of the plight of threatened species.

There is considerable scope for using video to evaluate the effectiveness of conventional techniques. In particular, video can provide a means of exploring species-specific behavioural responses to different survey methods (e.g. Grant *et al.* 2004), or provide checks on our understanding of the relative abundance of species, extremes in their distribution and abundance, and cryptic habitat use. To date, most studies in Australia have used underwater cameras in a field context to compare with and/or complement conventional sampling methods (e.g. netting, electrofishing), or applied video directly to assess the abundance of a key freshwater species, or investigate patterns of species richness. These studies have revealed that camera-based techniques can be superior to conventional sampling techniques, particularly for hard to catch species (e.g. Ebner & Morgan 2013); but that manual survey methods (e.g. trained human observers working on snorkel) could provide an equally effective or superior technique (Fulton *et al.* 2012; Ebner *et al.* 2014). Where video has a similar efficacy to traditional gear, the increasing affordability and image quality of portable cameras (e.g. GoPro®) is making the former an increasingly attractive option, particularly where equipment and training costs are prohibitive. For instance, boat electrofishing is a specialised and expensive outlay for short-term student projects. The complementary role of video as an additional sampling method, and a means of assessing the effectiveness of conventional techniques (e.g. Grant *et al.* 2004), means that video should be considered even when equipment and expertise costs are not a limiting factor. Indeed, in many cases, video may be the only viable option for exploring the ecology of freshwater species in the wild where human access is compromised or observer safety is at risk.

The general consensus amongst the authorship group was that underwater video has a major role to play in developing an understanding of the behaviour of freshwater fishes and crustaceans in Australia. In part, this is because many commonly used sampling methods are capture-based and not well suited to behavioural observation. Telemetry methods (radio, acoustic, passive integrated transponder based techniques) provide a notable exception, but video has the capacity to garner different types of behavioural information (e.g. predation, predator avoidance, competitive interaction) because it acts at finer spatial and temporal scales and can be used to study non-tagged individuals and species.

For these reasons both telemetry and video can play complementary and synergistic roles (e.g. Butler & Rowland 2009; Cooke *et al.* 2001). From a practical perspective, video has a bright future in elucidating interactions between aquatic species and humans (e.g. fishways, anglers, habitat restoration). There is also major potential for overcoming biases or at least confirming the relevance of laboratory based studies of aquatic fauna by conducting field based underwater video.

While cameras have facilitated laboratory and microcosm studies of freshwater fauna in Australia for several decades (e.g. Sandeman 1985; Richards & Bull 1990; Manger & Pettigrew 1995), the field-based video study of freshwater fishes and crustaceans in Australian freshwater ecosystems has only arisen in the past decade. Initially, this included use of analogue video recorded on magnetic film and powered by large gel-cell batteries (Butler & Rowland 2009; Ebner *et al.* 2009), and then, in time, moved to more portable media such as handheld digital cameras (e.g. Fulton *et al.* 2012). The reduced cost and size of cameras is poised to enable much wider use and/or greater replication across habitat types, times and/or sites. In turn this is likely to provide significant improvements for researching fishes and crustaceans since the limited field of view of a single camera is highly restrictive. Critical thinking is required in deciding on camera deployment strategies according to tradeoffs with cost, the potential risk of observer effects and pseudo-replication. Mobile cameras including towed cameras, manned underwater vehicles (e.g. Jones 2009) and animal-borne video (e.g. Heithaus *et al.* 2001) provide alternatives. Additionally, film has the capacity to facilitate communication of science and information about the natural world to the public. More than that, through evolving citizen science initiatives, such as crowd-sourcing, there is scope for involving people in data collection and processing phases of underwater video research. From a conservation perspective, this may just be the greatest opportunity for video-based ecology.

CONCLUSIONS

A small but steady number of video-based studies of Australian freshwater fish and crayfish has emerged during the past decade. These studies have included both temperate and tropical Australia. Encouragingly, other research is underway in provinces that have not previously been studied by video methods (e.g. Kimberley, Tasmania). There is much promise for video-based ecological investigations in upland lotic systems where clear water conditions often prevail and certain taxa attain their greatest species richness (e.g. spiny crayfish *Euastacus* spp., fishes of the Galaxiidae). To date, there have been no published applications from natural lentic systems in Australia despite promising research overseas (e.g. Mueller *et al.* 2006). There is clearly scope for the application of video in swamps and lakes with good visibility. There is also scope to use unmanned underwater vehicles (e.g. Jones 2009) and animal-borne video (e.g. Heithaus *et al.* 2001).

In the future we see video becoming a standard technique for surveying a broad diversity of freshwater fauna in clear water systems in Australia and elsewhere.

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The critically endangered hairy marron, *Cherax tenuimanus* Smith, 1912: A review of current knowledge and actions required to prevent extinction of a species

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The hairy marron, *Cherax tenuimanus* Smith, 1912, is a freshwater crayfish endemic to the Margaret River catchment in the south-west of Western Australia (Southwestern Province). Once abundant throughout its native range, *C. tenuimanus* is being rapidly replaced by the more widespread smooth marron, *Cherax cainii* Austin, 2002; to the extent that *C. tenuimanus* is now critically endangered. To enable policy makers to formulate a suitable recovery plan, there are key questions that need to be answered surrounding the biology and ecology of both species, particularly where the range extension of *C. cainii* has resulted in the two species existing in sympatry. The paucity of knowledge is further confounded by considerable historical confusion surrounding their morphological differentiation, nomenclature, and indeed their taxonomic classification as separate species. As a prelude to management planning, we provide a review of *C. tenuimanus* taxonomy, drawing particular attention to areas of confusion and disagreement in published literature. This review also highlights gaps in our understanding of the mechanism behind the decline of hairy marron and provides direction for future research and actions required to enhance the conservation of this critically endangered species.

KEYWORDS: conservation, *Cherax cainii*, freshwater crayfish, Margaret River, endemic, Western Australia, south-west, smooth marron

INTRODUCTION

Marron are large freshwater crayfish endemic to the south-west of Western Australia, of which two species are currently recognised. The most widespread species, the smooth marron, *Cherax cainii* Austin, 2002, occurs over much of the south-west of Western Australia where it forms the basis of a popular recreational fishery and aquaculture industry (Morrissy 1978). In contrast, a second protected and critically endangered species, the hairy marron, *C. tenuimanus* Smith, 1912, has a range restricted to the Margaret River catchment (Austin & Ryan 2002).

The Margaret River from of marron was identified as vulnerable in 1990 (Horwitz 1990a). Following reclassification as a distinct species, *C. tenuimanus* was identified as imminently threatened with extinction (Molony 2002). Consequently the species was listed as critically endangered at the state level under the Western Australian *Wildlife Conservation Act 1950* in 2005 and at the national level under the *Commonwealth of Australia Environment Protection and Biodiversity Conservation Act 1999* in 2006. Most recently *C. tenuimanus* has received international recognition and has been listed as critically endangered by the IUCN, a category that identifies it as facing a very high risk of extinction in the wild (Austin & Bunn 2010; IUCN 2001).

A draft plan to direct recovery actions for *C. tenuimanus* was developed by the Western Australian Department of Fisheries. The plan outlined ongoing or future recovery actions, however, there remain a number of key knowledge gaps that have hindered the implementation of conservation measures for the species.

This review summarises current knowledge on the ecology, taxonomy and conservation challenges of *C. tenuimanus* in order to inform a science-based approach to future management activities aimed at preventing any further decline of the species. Specifically, it will clarify historical work on the taxonomy based on morphology, and genetic analysis, and how it has contributed to the current taxonomic status of the species. It also addresses difficulties in differentiating between the two species and their hybrids in the field, and places quantitative data on distribution and abundance in the appropriate context, while providing a synthesis of *C. tenuimanus* population biology and ecology; discussing real and potential threats in the context of data derived from both captive and wild stocks; and propose conservation actions required to conserve *C. tenuimanus*.

Taxonomic recognition of *Cherax tenuimanus* and *Cherax cainii* as distinct species – an historical perspective

The history of the type material and designation of type specimens is controversial; the classification of marron as two separate species has been challenged (de Graaf *et al.* 2009) and the change to the accustomed usage of the name *C. tenuimanus* from the widespread form to the restricted form has been questioned (Molony *et al.* 2006). This review is undertaken in accordance with the designation of two species and the specific naming proposed by Austin and Ryan (2002).

Common names have been less controversial and were formally assigned at the "Scientific Workshop on the Margaret River Marron" (Koenders 2002); the Margaret River form was designated as the "hairy marron". The other form, which is endemic to the Southwestern Province and has been translocated within Western Australia, as well as across Australia and throughout the world (Shipway 1951; Morrissy 1978; Horwitz 1990b), received the common name "smooth marron".

Morphological evidence for recognition of distinct species

A single species of marron, *Cherax tenuimanus*, was originally described in 1912 (Smith 1912). Three subsequent studies of *Cherax* taxonomy also referred to only a single species (McCulloch 1914; Clark 1936; Riek 1967). In 1986, marron were split into two sub-species based on differences in electrophoretic and morphological characteristics between animals from Margaret River and the widespread form (Austin 1986). The form endemic to Margaret River was named *C. tenuimanus tenuimanus* and was distinguished by; clusters of long setae on the cephalothorax and sometimes the abdomen, a strongly raised median carina extending to the cervical groove, and a thorax without numerous tubercles (Austin 1986). The widespread form was designated as requiring a new sub-specific epithet and was identifiable by an absence of distinct long setae and the presence of numerous distinct tubercles on the thorax (Austin 1986). Subspecies classification was maintained in subsequent marron classifications (Horwitz 1995b; Austin & Knott 1996).

In 2002, the Margaret River form was elevated from sub-species to species based on a review of allozyme data collected intermittently during a 20-year period from 1979 to 1998, and the morphology of each species (Austin & Ryan 2002). The Margaret River form was designated as *C. tenuimanus*, and the widespread smooth form was assigned the new name *Cherax cainii* (Austin & Ryan 2002). Justification for this was based on the first published reference to marron listing the locality for *C. tenuimanus* as Margaret River (Smith 1912).

Confusion and controversy surrounding morphology and taxonomy

Smith (1912) examined more than one specimen of marron provided to him by Mr Woodward, the then Director of the Western Australian Museum and Art Gallery, as well as specimens in the British Museum. No specimen numbers were provided by Smith (1912) and the only other information regarding the origin of materials examined was his listing of the locality as Margaret River (Table 1). The initial description and drawings (Smith 1912) are not typical of the Margaret River form of marron described in 2002 (Austin & Ryan 2002) as only inconspicuous hairs are mentioned and no setation is present in the 1912 illustrative plate. However, the illustration does appear to have a median carina extending to the cervical groove; a trait of the Margaret River form of marron (Table 1) (Horwitz 1995b; Austin & Ryan 2002).

Subsequent taxonomic descriptions of marron failed to provide specimen numbers for the material examined (Table 1) (McCulloch 1914; Clark 1936). Samples examined by McCulloch (1914) were provided by Mr Woodward of the Western Australian Museum and Art Gallery and included specimens from outside of the Margaret River. The 1914 illustration of *C. tenuimanus* (*sensu stricto C. cainii*) (McCulloch, 1914) is typical of *C. cainii* as described in Austin and Ryan (2002) (Table 1), although the description mentions the median carina may run back to the cervical groove, a trait of *C. tenuimanus* (Horwitz 1995b; Austin & Ryan 2002). In contrast, a 1936 publication on Australian crayfish, which also examined marron specimens from outside the Margaret River, described *C. tenuimanus* as having a "densely hirsute carapace and abdomen", characteristics that are clearly those of the Margaret River form (Table 1) (Clark 1936).

The absence of specimen numbers prevents subsequent researchers identifying the material examined. A search of collections in the Natural History Museum (London) and the Western Australian Museum, was unsuccessful in locating any record of a holotype collected by Smith (Molony *et al.* 2006). In the absence of a designated type specimen, a lectotype was assigned in 1969 after examination of a marron of "about 11 inches" in the British Museum, which was assumed to be part of the materials examined by Smith (1912) based on size (Riek 1969). In contrast to the historic publications, the work that resulted in splitting *C. tenuimanus* into two species clearly stated which specimens were examined (Austin & Ryan 2002). The specimens examined included WAM C 127 (= WAM 4131), which was assumed by Austin and Ryan (2002) to be the holotype for *C. tenuimanus*; despite Smith (1912) not designating a holotype. In accordance with the International Code of Zoological Nomenclature (ICZN 2000) both a lectotype and a holotype cannot exist, however we do not attempt to address this situation with this manuscript.

The species nomenclature designated by Austin and Ryan (2002) was considered to conflict with the accustomed usage of *C. tenuimanus* referring to the widespread smooth species, and a reversal of the species names was proposed (Molony *et al.* 2006). The proposal did not mention the existence of the lectotype, and based on the evidence provided, it was not upheld by the International Commission on Zoological Nomenclature (ICZN) (ICZN 2008). Therefore the specific names and type specimens remained as those designated by Austin and Ryan (2002): type specimens for *C. cainii* (WAM C 28348) and for *C. tenuimanus* (WAM C 127) (ICZN 2008).

Genetic evidence for recognition of distinct species

An initial electrophoretic comparison of marron from Margaret River with those of Inlet River found the two populations to be conspecific (Austin 1979). However, all following studies of genetic relationships between marron from separate river systems provide strong support for the differentiation of the Margaret River form of marron from all other types. An analysis of allozyme variation in marron found that the Margaret River population was electrophoretically distinct at three loci (Austin & Knott 1996). Examination of three dinucleotide microsatellite loci across 88 animals to determine genetic distance between five subpopulations, also found Margaret River animals to be distinct from all

Table 1 Summary of the taxonomic studies of marron. N/A= not applicable.

	Smith 1912	**McCulloch 1914**	**Clark 1936**	**Riek 1967**	**Riek 1969**	**Austin & Ryan 2002**	
Species listed	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. cainii*
Type specimen or materials examined clearly given?	No	No	No	Yes "*Type*.–In the British Museum (Natural History), London."	Yes "*Type*.–The only specimen of the type series located in BM is the one of "about 11 inches". This male specimen, No.1968:221, cephalothorax length 125mm (overall body length 280mm), is selected as the lectoholotype." BM = "British Museum (Natural History), London."	Yes "*Holotype*. ♂ 62.7 mm OCL, Margaret R., Western Australia, 2.iii.1911, coll. B. Lipfert, WAM C 127 (WAM 4131)."	Yes "*Holotype*.♂, 84.8mm OCL, from Scott R., Brennan Bridge, Scott R. Road, 12 km north-east of Augusta, south-western Western Australia, coll. C. Austin 14.xii 1998, Western Australian Museum (WAM) C 28348"
If no to above, what information is provided?	"The largest specimen measures 6 ½ inches. Specimens in British Museum about 11 inches."	"Of the series examined the greater number were obtained in the Harvey River, seven miles above Harvey; one is from Korijekup, Harvey River; one from Margaret River; One from Balingup Brook; and three from the Warren River"	"With the exception of seven species the types or paratypes of each species have been examined" pg5. As no type locality is given for *C. tenuimanus* specimens, it is assumed that this is one of the seven species for which the type was not examined.	N/A	N/A	N/A	N/A
Type locality clearly given?	No	No	No	Yes "*Type Locality*.–Margaret River, Western Australia."	Yes "*Type locality*.–Margaret R., W.A."	"Margaret R., Western Australia"	"Scott R., Brennan Bridge, Scott R. Road, 12 km north-east of Augusta, south-western Western Australia"

Table 1 (cont.)

	Smith 1912	**McCulloch 1914**	**Clark 1936**	**Riek 1967**	**Riek 1969**	**Austin & Ryan 2002**	
Species listed	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. cainii*
If no, what information is provided?	"*Locality*.– Margaret River, Western Australia" is listed, but this is not clearly stated as the type locality.	"Of the series examined the greater number were obtained in the Harvey River, seven miles above Harvey; one is from Korijekup, Harvey River; one from Margaret River; One from Balingup Brook; and three from the Warren River"	"*Habitat.– Western Australia:* Margaret River (Miss H. Alexander, 1936) ; Harvey River; Korjekup; Kojonup; Balingup Brook; Warren River; Blackwood River; Katanning."	N/A	N/A	N/A	N/A
Origin of biological specimens clearly stated?	No	Yes – most material was received in January 1912 from Mr. Bernard H. Woodward, Director of the Western Australian Museum"	No	"The illustrations are based on a specimen from Kalgan", colour is based on "specimens from Beedelup Falls, near Pemberton"	No – refers to Riek (1967).	Yes – all material from Western Australia Museum	Yes – all material from Western Australia Museum
If no, what information is provided?	Specimens from WA provided by Mr. Woodward of Perth	N/A	"*Habitat.– Western Australia:* Margaret River (Miss H. Alexander, 1936) ; Harvey River; Korjekup; Kojonup; Balingup Brook; Warren River; Blackwood River; Katanning." These locations largely correlate with those listed by McCulloch 1914 whose specimens originated from the Western Australian Museum.	N/A	N/A	N/A	N/A
Quantity of specimens examined clearly given?	No	Yes, "A well graduated series of forty specimens, ranging from 57-296mm."	Yes – "12 specimens examined".	No	No – refers to Riek (1967).	Yes – 31	Yes – 62
If no, what information is provided?	"The largest specimen measures 6 ½ inches. Specimens in British Museum about 11 inches". Therefore more than one examined.	N/A	N/A	"Illustrations are based on a specimen from Kalgan", colour is based on "specimens from Beedelup Falls, near Pemberton". Therefore more than one. examined.	N/A	N/A	N/A

Species assignment based on description*	Unclear	Unclear	*C. tenuimanus*	Unclear	Unclear	*C. tenuimanus*	*C. cainii*
Justification for above*	Smith describes "numerous groups of short inconspicuous hairs". Austin and Ryan (2002) describe *C. cainii* as having "short inconspicuous setae". Preserved specimens of *C. tenuimanus* also have short inconspicuous setae (Senior author, pers. obs.). Smith describes "a few small tubercles on the branchiostegites". Austin and Ryan describe *C. tenuimanus* as having small-moderately sized tubercles" as opposed to the "large conspicuous tubercles" of *C. cainii.*	The majority of specimens originated outside Margaret River, therefore *C. cainii.* Median carina "may run back to the cervical groove" typical of *C. tenuimanus*, however, the median carina may also "terminate well before that point", typical of *C. cainii.*	"Entire carapace densely hirsute" and "entire abdomen more or less densely hirsute."	Diagnostic features that would enable discrimination between the two species are not mentioned.	Diagnostic features that would enable discrimination between the two species are not mentioned.	Diagnostic paper on morphology of *C. tenuimanus*	Diagnostic paper on morphology of *C. cainii*
Species assignment based on illustration*	Unclear	*C. cainii*	Unclear	*C. cainii*	No Illustration	*C. tenuimanus*	*C. cainii*
Justification for above*	Illustration in Smith 1912 (PL. XXII) shows a continuous median carina extending to the cervical groove, typical of *C. tenuimanus.* It lacks large conspicuous tubercles on the branchiostegites that are typical of *C. cainii.* No hairs are present in the illustration – diagnostic of *C. cainii.*	Illustration in McCulloch 1914 (Plate XXXIV) shows no setae. Branchiostegites possess large conspicuous tubercles and the abdomen has moderate-large tubercles typical of *C. cainii.*	Plate (IV) is a line drawing of the cephalon only.	No hairs are present. Tubercles on areola dorsally present, although reduced as specimen appears to be a sub-adult.	N/A	Diagnostic paper on morphology of *C. tenuimanus*	Diagnostic paper on morphology of *C. cainii*

*Using characteristics defined by Austin & Ryan (2002) as different between the *C. tenuimanus* and *C. cainii.*

other marron populations and deserving of conservation (Imgrund *et al.* 1997; Imgrund 1998). Further studies comparing 12s mitochondrial DNA sequence resulted in population subdivisions that were entirely consistent with those found in 1996 (Nguyen *et al.* 2002). Two haplotypes were present, one haplotype was exclusive to marron from the Margaret River and a second haplotype was associated with all other locations (Nguyen *et al.* 2002). Subsequent analysis of four mitochondrial DNA loci (12s, 16s, Cyt *b*, and CO1) further confirmed *C. tenuimanus* from the Margaret River system to be phylogenetically distinct from all other locations (Munasinghe *et al.* 2003).

The argument for classification of *C. tenuimanus* and *C. cainii* as separate species was based on testing of the hypothesis that if the taxonomic conclusions of Austin and Knott (1996) were correct and the two marron forms were sub-species, then allozyme data should reveal a high degree of genetic mixing and substantial introgression of alleles (Austin & Ryan 2002). Although hybrids were present, their abundance was not representative of that expected from random mating, suggesting hybrids either had reduced viability, or the marron forms showed assortative mating behaviours, thus providing justification for the description of two separate species (Austin & Ryan 2002). This argument has been challenged by subsequent studies that have found higher proportions of hybrids (Bunn 2004, de Graaf *et al.* 2009), however no empirical testing has been attempted.

Identification of *Cherax tenuimanus* and *Cherax cainii* in practice

Marron are easily distinguished from all other *Cherax* species in the south-west of WA because they are considerably larger and possess spines on the telson (Horwitz 1995b). A combination of morphological characteristics can be used to differentiate the two marron forms (Austin & Knott 1996) and a formal description of each species is provided by Austin and Ryan (2002). The most distinctive of the differences are: the presence of a median carina that extends continuously, without depression, to the cervical groove; prominent tufts of long recumbent setae; and the absence of tuberculation on the areola on *C. tenuimanus* (Austin & Ryan 2002).

Field identification of the two marron species in Margaret River based on morphological differences is confounded by the presence of hybrid/backcrossed animals displaying a range of characteristics from each of the species (Lawrence 2002), and inconsistent variations in morphology due to sex, maturity, and size (Bunn *et al.* 2008). An attempt to improve the accuracy of field identification of pure and hybrid animals was made utilising the morphology of the median carina, and presence or absence of clusters of setae (Bunn *et al.* 2008). Using these characters, approximately 90% of *C. cainii* and *C. tenuimanus* could be identified correctly; however, correct identification of hybrids was more difficult, with an accuracy of only approximately 70% (Bunn *et al.* 2008). The difficulty associated with identification has obvious implications for the accuracy of population data and breeding studies where morphology has been used to identify the species. This is the same data that has underpinned management decisions to date and an improved method of identification is required to enhance on ground conservation actions (Bunn *et al.* 2008).

Current biological and ecological knowledge of *Cherax tenuimanus*

Wild population data and captive breeding work may suffer from difficulties in identification of hybrids. All previous studies have used the best characteristics for identification of hairy marron based on knowledge at the time of undertaking their work. However, without definitive genetic testing being undertaken, a level of incorrect identification may have occurred across all those studies.

Distribution and abundance

Prior to 1980, only *C. tenuimanus* was present in the Margaret River (Austin & Ryan 2002). Introduction of *C. cainii* into Margaret River is thought to have occurred in the early 1980s (Austin & Knott 1996). It is not known if the introduction of *C. cainii* was from a single event, multiple events, or even if it is ongoing. In less than 20 years, *C. tenuimanus* has been wholly replaced at the site where *C. cainii* was first located within the Margaret River (Austin & Ryan 2002). The upstream spread of *C. cainii* has been rapid, and by 2002, *C. tenuimanus* had been replaced in the middle reaches of the river (Bunn 2004; de Graaf *et al.* 2009). Marron populations in the upper reaches were wholly *C. tenuimanus* in 1995, however, by 2002 they contributed only 30% of the marron population in this stretch of river (Bunn 2004). Estimates of the population of *C. tenuimanus* have continued to decline and now range between 5 to 25% of marron in the upper Margaret River (DoF unpublished data).

Growth and survival

Growth rate of *C. tenuimanus* in the wild has not been thoroughly investigated and the only data on growth comes from a single pool located in the upper reaches of the Margaret River, Canebrake Pool (Bunn 2004). Within this pool, both *C. tenuimanus* and *C. cainii* reached a similar size, although *C. cainii* grew at twice the rate of *C. tenuimanus* (0.063 vs. 0.033 mm.day^{-1}, respectively) (Bunn 2004). These results are based on a very small number of individuals and are skewed by the inclusion of animals recaptured in the same sampling period in the analysis (Bunn 2004). Attempts to estimate growth based on modal peaks from consecutive cohorts, are likely to be inaccurate given the small sample size and lack of clear cohorts (Bunn 2004), therefore these growth values are not discussed herein. No information on comparative survival of *C. tenuimanus* in the wild is available and both growth and survival of wild populations thus requires further investigation.

Data on growth rate in captivity is more abundant. Juvenile *C. tenuimanus* grew quickly and at the time of stocking into grow-out ponds, were larger than offspring of *C. cainii* from five different rivers (Lawrence *et al.* 2007a). At the end of the two years of grow-out, survival did not differ and *C. tenuimanus* were of similar size to the *C. cainii* from the Kent, Shannon, Donnelly, and Warren Rivers (Lawrence *et al.* 2007a). Growth rate of *C. tenuimanus* in captivity was approximately four fold that calculated for wild *C. tenuimanus* (0.11 vs. 0.033 mm.day^{-1}) and double that for wild *C. cainii* in Margaret River (Bunn 2004; Lawrence *et al.* 2007a); most likely a result of diet supplementation of captive animals with high quality feed pellets (C. Lawrence pers. comm.). Unlike the wild population, captive male *C. tenuimanus* were significantly larger than females (82.70g S.E. ± 1.65g vs. 55.87g S.E. ± 3.97g after 2 years of grow-out (n=30)) (Lawrence *et al.* 2007a). Survival of *C. tenuimanus* in captivity was similar to that of *C. cainii* from various rivers, even when all were grown communally, demonstrating an equal ability to compete (Lawrence *et al.* 2007c).

Reproduction

Despite concerns about the conservation status of this species in 2002 (Koenders 2002), the ongoing captive breeding of the species, and the production of a draft recovery plan in 2008, knowledge of the reproductive biology of *C. tenuimanus* has progressed little. There is some evidence of a difference in the timing of reproduction for each species based on differences in the timing of reduced catchability linked with reproduction (Bunn 2004) and of the possibility of later gonadal maturation in female *C. tenuimanus* (J Bunn pers. comm.; DoF unpublished data). This is an area requiring further investigation as it has numerous implications for conservation actions.

Nothing is known about reproductive success of wild *C. tenuimanus*. The only data comes from captive breeding (Morrissy & Cassells 1990; Henryon 1995; Lawrence *et al.* 2007a). Both Lawrence *et al.* (2007a) and Henryon (1995) selected animals that possessed hairs and a continuous median carina (C. Bird pers. comm.; M. Henryon pers. comm.) in an attempt to breed only *C. tenuimanus*. Lawrence *et al.* (2007a) further tried to reduce the chance of using hybrids by only collecting animals from the upper reaches where the *C. tenuimanus* population was in the highest proportion, and by sourcing *C. tenuimanus* from an isolated population transferred from the Margaret River onto a private property in the 1970's. Early attempts at breeding marron from Margaret River resulted in very low rates of breeding, 2–8% (Morrissy & Cassells 1990; Henryon 1995) compared to 68.5% for long term domesticated stock of *C. cainii* (Morrissy & Cassells 1990). Despite best efforts, it is possible that hybrids with *C. tenuimanus* characteristics may have been included (Horwitz 1994). Greater success was later had by Lawrence *et al.* (2007a) where 53% of females captured from the Margaret River were mated successfully. Captive breeding found an inverse correlation between the percentage of berried *C. tenuimanus* females and weight, indicating a decrease in breeding frequency with size, a trait similar to *C. cainii* from various rivers (Lawrence *et al.* 2007a). All marron produced equal sex ratios of juveniles (Lawrence *et al.* 2007a).

Hybridisation

There is clear evidence of hybridisation between *C. tenuimanus* and *C. cainii* in the Margaret River (Imgrund *et al.* 1997; Austin & Ryan 2002; Nguyen *et al.* 2002) and in captivity (Henryon 1995; Lawrence *et al.* 2007b). Breeding experiments crossing *C. tenuimanus* with *C. cainii* have shown that the river of origin and the sex of the parent from that river, impacted the rates of successful reproduction (Lawrence *et al.* 2007b).

Fertile hybrids have been produced in captivity (Lawrence *et al.* 2007b) and electrophoresis techniques used to identify *C. tenuimanus, C. cainii,* and hybrid marron in the Margaret River have also identified the presence of F2 back crosses in the wild, demonstrating the fertility of hybrids in the wild (Bunn *et al.* 2008). Growth comparisons of hybrids in captivity found that, with the exception of one instance where Margaret River hybrids (Margaret River *C. tenuimanus* females, and Kent river *C. cainii* males) grew 32% faster than its parents, hybrid offspring typically grow 30–63% slower than the parents (Lawrence *et al.* 2007b).

Behaviour

The two species of marron show some slight variations in behaviour. A laboratory investigation of agonistic interactions between *C. tenuimanus* and *C. cainii* from the Warren River found size was the main factor determining dominance for males (Jenour *et al.* 2007). When animals were the same size, both marron types showed a similar frequency of agonistic interactions (Jenour *et al.* 2007). Female *C. tenuimanus* were less aggressive than *C. cainii* when of equal size or smaller (Jenour *et al.* 2007). When female *C. tenuimanus* had the advantage of size, aggressive interactions were equal, a pattern not seen in males (Jenour *et al.* 2007) nor in studies on crayfish of other species (Bovbjerg 1956; Lowe 1956; Vorburger & Ribi 1999).

Use of shelter for both *C. tenuimanus* and *C. cainii* was minimal when each animal was housed individually and didn't change for males when held in sympatry regardless of relative size (Jenour *et al.* 2007). Female *C. tenuimanus* and *C. cainii* showed a high preference for shelter when kept separately and when housed together with limited shelter, shelter occupancy was higher for marron with a size advantage (Jenour *et al.* 2007).

Conservation of *Cherax tenuimanus*

Summary of known threats

Investigations into the biological characteristics of *C. tenuimanus* in the wild have been confounded by small sample sizes and discontinuous data. In addition, given the error associated with identifying hybrids (see Bunn *et al.* 2008), all studies that have not used genetically tested animals risked the inclusion of hybrids in their research. Despite these caveats, previous work provides valuable insight on the mechanisms behind the decline in *C. tenuimanus* numbers.

Hybridisation is considered one of the major factors causing a decline in the *C. tenuimanus* population (Horwitz 1995a; de Graaf *et al.* 2009), however, other authors have found fewer hybrids than would be expected from random mating (Austin & Ryan 2002). Captive breeding and genetic studies have demonstrated that fertile hybrids can occur, but success of *C. tenuimanus* and *C. cainii* crosses in producing hybrids depends on the river of origin of *C. cainii* and its sex (Lawrence *et al.* 2007b). Where *C. tenuimanus* have been wholly replaced, the population lacks any hybrids at all (Bunn 2004).

Therefore the production of hybrids itself may not be causing the decline, rather reproductive interference may be the mechanism impacting the *C. tenuimanus* population. Parental heritage of hybrids should be examined to elucidate the role of hybridisation. Differences in reproductive potential may also factor in the decline of *C. tenuimanus*. If the low rate of breeding of wild *C. tenuimanus* compared to wild *C. cainii* held in captivity is reflective of a pattern in the wild, this may play a significant role in the decline of *C. tenuimanus*. All aspects of reproductive biology of *C. tenuimanus* and *C. cainii* in sympatry require further investigation in wild populations.

Direct competition is unlikely to be a driver of the decline as both species have demonstrated an equal ability to compete when raised communally (Lawrence *et al.* 2007c). However, an investigation of female interspecific intrasexual competition has shown *C. cainii* to be more aggressive (Jenour *et al.* 2007). Replication of these behaviours in the wild could impact female *C. tenuimanus* directly through losing competitive interactions around shelter acquisition, and/or it could potentially result in the exclusion of *C. tenuimanus* females from food resources or mates.

An environmental replacement mechanism was proposed by Bunn (2004) that suggested the correlation between the presence of farmland bordering the Margaret River and the absence of *C. tenuimanus* in that stretch of river. Bordering land use may have an impact, although *C. tenuimanus* were found throughout Margaret River, prior to the introduction of *C. cainii*, whilst still influenced by the current land use regimes. In addition, the spatial distribution of *C. cainii* was also consistent with a pattern of upstream spread from the point of initial introduction recorded by Austin and Knott (1996).

Knowledge gaps and conservation actions

There are still many aspects of marron ecology in the Margaret River where no conclusions can be drawn due to a paucity of data, e.g. timing of breeding, growth rates, and movement. Without this knowledge, it is difficult to determine the mechanism behind the replacement of *C. tenuimanus* by *C. cainii* and in turn, any recovery actions are likely to be met with limited success.

Development and implementation of an effective, science-based, well-resourced recovery plan is essential for preventing extinction of the critically endangered *C. tenuimanus*. The following key principles have been identified as actions that are achievable with current knowledge and their chance of success is not necessarily linked to understanding the replacement mechanism. Once completed, these actions will form the platform for future actions that will aim to enhance the wild *C. tenuimanus* population, e.g. restocking or investigations into methods for reduction of the *C. cainii* population.

Development of improved field identification techniques to support practical management strategies

The success of practical intervention strategies relies on rapid and accurate field identification of genetically 'pure' *C. tenuimanus*. Field identification based on morphological differences however, has been confounded by the presence of hybrid and backcrossed animals displaying a range of characteristics from each of the species (Lawrence 2002), and possible variations in morphology due to sex, maturity, and size (Bunn *et al.* 2008). The primary and most confronting problem in *C. tenuimanus* conservation is thus the absence of an appropriate method of accurate differentiation between *C. tenuimanus*, *C. cainii*, and the resulting hybrids and back-crosses. Initial classification of *C. tenuimanus* and *C. cainii* into two separate species was based on allozymes; however this technique is not well suited to providing identification in the field. An attempt to generate a key for identification used a small number of characteristics and achieved reasonable success, although it highlighted the need for further improvement (Bunn *et al.* 2008). An urgent need therefore exists for the development of a validated, practical, accurate, and quantifiable method of field identification.

Development of an improved understanding of the genetic purity of remaining *Cherax tenuimanus* population

Given the prolonged period of sympatry of *C. tenuimanus* and *C. cainii* populations within the Margaret River, genetic introgression between the species may have occurred. Therefore a strategy to determine the level of "purity" of remaining *C. tenuimanus* is required before any attempt to establish a breeding population for restocking can begin. Genetic studies involving microsatellites are currently underway to identify the extent of genetic introgression between sympatric *C. tenuimanus* and *C. cainii* populations with the aim of identifying individuals most suited to a captive breeding program (Kennington *et al.* 2013).

Establishment of a captive breeding population of *Cherax tenuimanus*

The recent and rapid decline of *C. tenuimanus* demonstrates that the establishment of a captive breeding population is essential. Some progress has been made in this regard with successful breeding from a population of genetically identified broodstock animals in the Department of Fisheries hatchery facility at Pemberton. Further work is required to ensure the purity of this population. In addition, establishing a captive breeding population of *C. tenuimanus* has to date proved more challenging than for their *C. cainii* counterparts for reasons largely unknown. Overcoming these limitations will be essential to producing animals in sufficient numbers to restock natural waterbodies where the species might be able to become self-sustaining once again.

CONCLUSIONS

Cherax tenuimanus have been rapidly replaced by *C. cainii* within the Margaret River to such an extent that they are now critically endangered (de Graaf *et al.* 2009; Austin & Bunn 2010). A lack of knowledge was highlighted at the *Scientific Workshop on the Margaret River Marron* (Koenders 2002) in 2002 and more than 10 years later many of the same knowledge gaps still exist. Much of what is known is derived from a small number of wild individuals, studies of marron in captivity, or assumed to be similar to *C. cainii*. The paucity of knowledge combined with confusion regarding taxonomy and identification has hampered the effective management of *C. tenuimanus* resulting in the continued decline in both its numbers and its range.

In order to provide an effective way forward to prevent extinction of *C. tenuimanus*, the draft hairy marron recovery plan needs to be revised and completed to include actions with measurable outcomes. With the dwindling numbers of *C. tenuimanus* in Margaret River, the first actions of the recovery plan should be improved methods of identification, determination of the purity of the remaining *C. tenuimanus* populations, and the establishment of a captive breeding population of pure *C. tenuimanus*. Subsequent actions need to address knowledge gaps in basic biology and determine the mechanism of decline, whilst at the same time enhancing the *C. tenuimanus* population and reducing the *C. cainii* population.

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Long live the King River Perchlet (*Nannatherina balstoni*)

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Exactly 100 years following the discovery of Balston's Pygmy Perch (*Nannatherina balstoni*) and its subsequent description from south-western Australia, it was added to the Australian Government's endangered species list due to a contraction of the species range and its low abundance relative to sympatric species. The current study aimed to determine the historical and contemporary geographical range of the species, to quantify its range reduction and prioritise areas for ongoing monitoring and management. The original common name of this species, the King River Perchlet, was derived from the type locality of the two syntypes deposited at the British Museum of Natural History. Only one syntype remains. Based on a review of published information and unpublished data held by the authors, the apparent contemporary area of occurrence of *N. balstoni* is now ~69% of its historical distribution. The remaining syntype from the King River represents the only known specimen from that system and the species is no longer known to occur there. Similarly, the species appears to have been extirpated from the Moore River at the northern limit of its range during the latter part of the 20th century, and presumably also from many rivers of the Swan Coastal Plain as well as Turner Brook in the extreme south-western corner of its range. Based on genetic differences between populations, it is proposed that the loss of these populations is likely to have resulted in an irreversible loss of evolutionary significant units. A recovery plan is critical for the management of the species, with on-ground surveys required in order to confirm ongoing population viabilities. Quantification of the numerous threats to the species (e.g. impacts of instream barriers, surface flow and groundwater reductions due to climate change and water extraction, riparian degradation, secondary salinisation and the presence of introduced species) is also required.

KEYWORDS: Balston's Pygmy Perch, Percichthyidae, south-western Australia, salinisation, endangered species

INTRODUCTION

Nannatherina balstoni was described by C.T. Regan in 1906 (Regan 1906). Exactly 100 years later, it was added to the threatened species list of the Australian Government. It is one of four freshwater fish species of the Percichthyidae that is endemic to the Southwestern Province of Western Australia (Morgan *et al*. 2011), a region known as a globally significant hotspot of endemism (Myers *et al*. 2000; Olson & Dinerstein 2002).

The type locality of *N. balstoni* is the King River, just east of Albany, from which two specimens were collected by G.C. Shortridge and presented to the British Museum by W.E. Balston in 1906. Regan (1906) placed *N. balstoni* in the Atherinidae where it remained until 1940, when it was placed in the Kuhliidae (Regan 1940). Kuiter and Allen (1986) later placed it in the Percichthyidae before it was positioned in the Nannopercidae a few years later (Allen 1989; Kuiter *et al*. 1996). At the turn of this century, Jerry *et al*. (2001) demonstrated that the pygmy perches are monophyletic with *Macquaria*, resulting in the placement of *N. balstoni* back into the Percichthyidae.

Whitley (1947) first assigned the common name King River Perchlet in reference to the type locality of the species. Since then, alternative names have included Balston's Perchlet (Merrick & Schmida 1984) and Balston's Pygmy Perch (Allen 1982, 1989) after W.E. Balston, who presented the first specimens to the British Museum.

Historically, and prior to surveys in the early 1990s (see Morgan *et al*. 1998), little was known regarding the extent of the distribution of the species, with the exception of a few specimens housed in various museums (see Table 1). For example, Coy (1979) and Allen (1982, 1989) broadly list the species as having a distribution that is limited to the streams, lakes, ponds and swamps between Two Peoples Bay and the Blackwood River, although Webster (1949) had also discovered the species from north of the Blackwood River in the Margaret River near Rosa Brook in 1948 (Table 1). Knowledge of the distribution of *N. balstoni* increased markedly during the 1980s and 1990s and was documented by Morgan *et al*. (1998), who reviewed all historical collection data and also identified 35 additional occurrence localities between Margaret River and Two Peoples Bay (Goodga River). These records include rivers, coastal swamps and several lakes throughout the

Table 1 Specimens of *Nannatherina balstoni* that are housed in the collections of various institutions, including year of collection and collector. Abbreviations for institutions are as follows: Western Australian Museum (WAM), South Australian Museum (SAM), Museum Victoria (NMV), Australian Museum (AM), British Museum of Natural History (BMNH), South African Institute for Aquatic Biodiversity (SAIAB), and the National Museum of Natural History (AMNH). * Indicates type specimens. # Specimen may be from WAM.

Institution	Specimen ID	Year of collection (and collector)
BMNH	* BMNH 1906.11.1.21-22	1906 (Shortridge, G.C.)
AM	I.13265, I.13266	1914 (?)
WAM	P.3075.001	1947 (Shipway, B.)
WAM	P.4033.001	1957 (Butler, W.H.)
WAM	P.5761.001	1958 (Butler, W.H.)
WAM	P.5514.001	1962(Butler, W.H.)
NMV	A5520	1964 (Littlejohn, M.J.)
NMV	A514	1966 (Frankenberg, R.)
AMNH	315892	1969 (Rosen)
AMNH	315892.5	1969 (Rosen)
WAM	P.25697.003	1976 (Allen, G.R.)
WAM	P.27149.001	1981 (Pusey, B.)
WAM	P.27025.001	1981 (Przybylski)
WAM	P.28655.002	1986 (Allen, G.R. & Berra, T.)
WAM	P.28656.002	1986 (Allen, G.R. & Berra, T.)
WAM	P.28658.003	1986 (Allen, G.R. & Berra, T.)
WAM	P.28659.002	1986 (Allen, G.R. & Berra, T.)
SAIAB	55471	1986 (Berra, T. & Allen, G.R.)
WAM	P.28641.003	1986 (Berra, T. & Cross, N.)
WAM	P.28644.004	1986 (Allen, G.R. & Berra, T.)
WAM	P.28652.003	1986 (Allen, G.R. & Berra, T.)
AMNH	# USNM 289205	1986 (Allen, G.R.)
WAM	P.30438.004	1992 (Jaensch, R.)
WAM	P.30439.003	1992 (Jaensch, R.)
WAM	P.30443.002	1992 (Jaensch, R.)
WAM	P.30441.002	1992 (Jaensch, R.)
WAM	P.30450.002	1992 (Jaensch, R.)
WAM	P.30453.002	1992 (Jaensch, R.)
WAM	P.30444.002	1992 (Jaensch, R.)
WAM	P.30446.002	1992 (Jaensch, R.)
SAM	F13624	2008 (Adams, M.)
SAM	F13625	2008 (Adams, M.)
SAM	F13626	2008 (Adams, M.)
SAM	F13627	2008 (Adams, M.)
SAM	F13628	2008 (Adams, M.)
SAM	F13629	2008 (Adams, M.)
SAM	F13630	2008 (Adams, M.)

region and the Western Australian Museum has a collection of the species from an outlying locality in the Moore River catchment in the north of the Southwestern Province.

The most comprehensive ecological study of the species was that by Morgan *et al.* (1995), who described its habitats and biology, which included diet, reproductive development, spawning period and cues, longevity, and growth. Gill & Morgan (1998) described the larval development, including the pronounced ontogenetic shift in diet through larval stages to the juvenile stage, when the species begins to feed almost exclusively on fauna derived from terrestrial sources (e.g. insects). Beatty *et al.* (2011) examined the salinity tolerance of the species, in light of its highly restricted distribution in the Blackwood River, and found it to be far less tolerant than the widespread but sympatric *Nannoperca vittata* and *Galaxias occidentalis*. Within the Blackwood River catchment, the region's largest by discharge, the species is known to migrate in and out of a single perennial stream for breeding (Beatty *et al.* 2014). This stream, Milyeannup Brook, is a groundwater dependent ecosystem and is not affected by the secondary salinisation which has severely impacted large sections of the Blackwood River catchment (Morgan & Beatty 2003; Beatty *et al.* 2011).

Although the common name for this species has changed over time, contemporary literature favours the name Balston's Pygmy Perch (e.g. Morgan *et al.* 1995, 1998, 2011; Gill & Morgan 1998; Allen *et al.* 2002; Yearsley *et al.* 2006; Morgan 2009; Beatty *et al.* 2011, 2014). The original common name, King River Perchlet, is no longer appropriate for two reasons. Firstly, the species is much more widespread than first believed, and secondly, it is believed to have been extirpated from the King River.

In addition to the King River, it is likely that the species has been lost from the Moore River catchment, at the northern limit of its distributional range (Morgan *et al.* 1998, 2011; Morgan 2009), where it was collected in January 1981 (Western Australian Museum specimen number P.27025.001), as well as from Turner Brook, where it has not been collected since the 1960s (Morgan *et al.* 2013) (see Table 1). Thus, we know of three populations that have likely been extirpated since the species was first discovered, but it has also likely been lost from much of the Swan Coastal Plain between the historical population at Moore River and the existing Margaret River population. These findings are based on the species being common in near-coastal wetlands throughout its range, most of which are now dewatered throughout the Swan Coastal Plain (see Morgan *et al.* 2011) as well as the record of a single specimen captured in the Collie River by L. J. Pen in the 1980s (L. Pen, pers. com.).

The loss of populations, severe range fragmentation, and a typically low abundance (e.g. Morgan *et al.* 1995, 1998), resulted in *N. balstoni* being listed in 2006 as *Vulnerable* under the Australian Federal Government's *Environmental Protection and Biodiversity Conservation Act 1999*, with the species concurrently listed as *Schedule 1* under the Western Australia State Government's *Wildlife Conservation Act 1950*. However, its extent of occurrence and area of occupancy has not been quantified.

A major component of any threatened species recovery plan is current distributional information so that key habitats can be prioritised for conservation and management. Over the last quarter of a century, there has been additional distributional information gathered. Here we aimed to collate all existing records of the species to ascertain its current and historical extent of occurrence and identify key populations and habitats. We hypothesised that the geographical range of the species has continued to decline. It is our hope that this information will prove valuable in developing and implementing conservation efforts to maintain remnant populations of this listed threatened species.

DETERMINING THE HISTORICAL AND CONTEMPORARY DISTRIBUTION

The historical distribution of *N. balstoni* was determined via an extensive search of published scientific literature and museum databases (see Results). We also contacted various museums regarding specimens they held, or to clarify uncertainties in database searches, for example missing location data. Other unpublished data from our own surveys, which commenced in 1992, were included in the analyses. In some publications, the exact locality of the collection was not given (e.g. Pusey & Edward 1990; Morgan *et al.* 1995); however, they were incorporated into later publications (e.g. Morgan *et al.* 1998) and were also used in the present analyses. A species distribution map was created using ArcGIS™ Desktop 10, and sites were separated based on whether they were collected prior to, or after, the commencement of our distributional surveys in 1992.

Extent of occurrence

Previously known sites of capture of *N. balstoni* were used to estimate its extent of occurrence in ArcGIS™ Desktop 10. Extent of occurrence (EOO) was determined using the distributional point data by constructing minimum convex polygons (α-hulls) following IUCN guidelines (IUCN 2011).

Two α-hulls were constructed from the data. The first was constructed using all historical EOO point data excluding the outlying historical Moore River population. The second was constructed using all historic data and included an assumed additional area of occupation based upon historical and remnant distributions of sympatric species as discussed in Morgan *et al.* (1998). The areas of the resulting polygons were determined. The IUCN guideline stating that internal angles of the polygons should not exceed 180° was relaxed in order to exclude unsuitable habitat, i.e., the marine environment.

RESULTS

Specimens of *N. balstoni* were located in the collections of the Western Australian Museum, South Australian Museum, Museum Victoria, Australian Museum, British Museum of Natural History (Figure 1), South African Institute for Aquatic Biodiversity, and the National Museum of Natural History (Table 1). Published literature detailing collections of *N. balstoni* included: Christensen (1982) (four sites); Pusey & Edward (1990) (five sites); Morgan (1993) (11 sites); Morgan *et al.* (1995) (three sites, exact localities not given but taken from Morgan (1993)); Morgan *et al.* (1996) (29 sites); Morgan *et al.* (1998) (35 sites, 29 of which were identical to those in Morgan *et al.* (1996)); Morgan & Beatty (2003) (two sites); Morgan & Beatty (2005a) (one site); Morgan & Beatty (2005b) (four sites); Beatty *et al.* (2006) (four sites); Morgan *et al.* (2010) (two sites); Beatty *et al.* (2011) (one site) and; Beatty *et al.* (2014) (four sites) (Figure 2).

Table 2 Assumed current (i.e. using historical species presence data excluding the extirpated Moore River population) and estimated historical (i.e. using historical species presence data with additional area of assumed past distribution) area of occurrence of *Nannatherina balstoni* in south-western Australia.

Point data description	Area of occurrence (sq. km)	Perimeter of occurrence (km)
Assumed current distribution	15867	726
Estimated historical distribution	22859	1366

There have been no records of *N. balstoni* from the King River since the syntypes of the species were originally collected there in 1906 (Table 1). A recent survey of Turner Brook, in the extreme south-western corner of the State, failed to detect *N. balstoni*, which was previously collected from that system by W.H. Butler on several occasions between 1957 and 1962 (Table 1, Figure 1) (Morgan *et al.* 2013). Similarly, there are no records of *N. balstoni* from the Moore River catchment since they were first collected there in 1981 by G.R. Allen.

The contemporary distribution of *N. balstoni* is approximately 69% of its historical area of occupancy (Table 2, Figure 2). The abundance of *N. balstoni* relative to sympatric species is typically low, but no studies have been published specifically to estimate population sizes. Studies that provide some indication of population size are restricted to those by Beatty *et al.* (2014) and to a lesser extent Morgan *et al.* (1995). However, the authors are conducting a study to quantify the abundance of sympatric percichthyids (i.e. Balston's Pygmy Perch, Western Pygmy Perch *Nannoperca vittata*, Little Pygmy Perch *Nannoperca pygmaea*, and Nightfish *Bostockia porosa*) in refuge pools in the Hay River, with preliminary results revealing that the abundance of the Balston's Pygmy Perch was only 0.3% of the total number of pygmy perches present. Aside from Milyeannup Brook (Beatty *et al.* 2014), this low level of abundance of the species appears typical throughout its range.

DISCUSSION

Based on the records collated here, the approximate 31% reduction in range of *N. balstoni* appears to have occurred during the last quarter of the 20th century. This reduction is due to the loss of the northernmost population in the Moore River, the loss of the Turner Brook population, and from the likely loss of populations along the Swan Coastal Plain. Further range contractions are suspected to have occurred due to human-induced secondary salinisation in many of the region's larger river systems that house this species such as the Blackwood River (e.g. Beatty *et al.* 2011, 2014). It is paramount that historical sites are re-surveyed, including those where limited data exist, those where capture methods were used that are less effective than current methods (i.e. fyke netting: with the first reported use of this method to target south-western Australian freshwater fish being from 2004 in the Blackwood River (Morgan & Beatty 2005b), as well as those that were once known to support robust populations (e.g. Morgan *et al.* 1995, 1998; Beatty *et al.* 2014).

Based on allozyme evidence, Murphy *et al.* (2010) found three distinct genetic lineages for *N. balstoni*, one

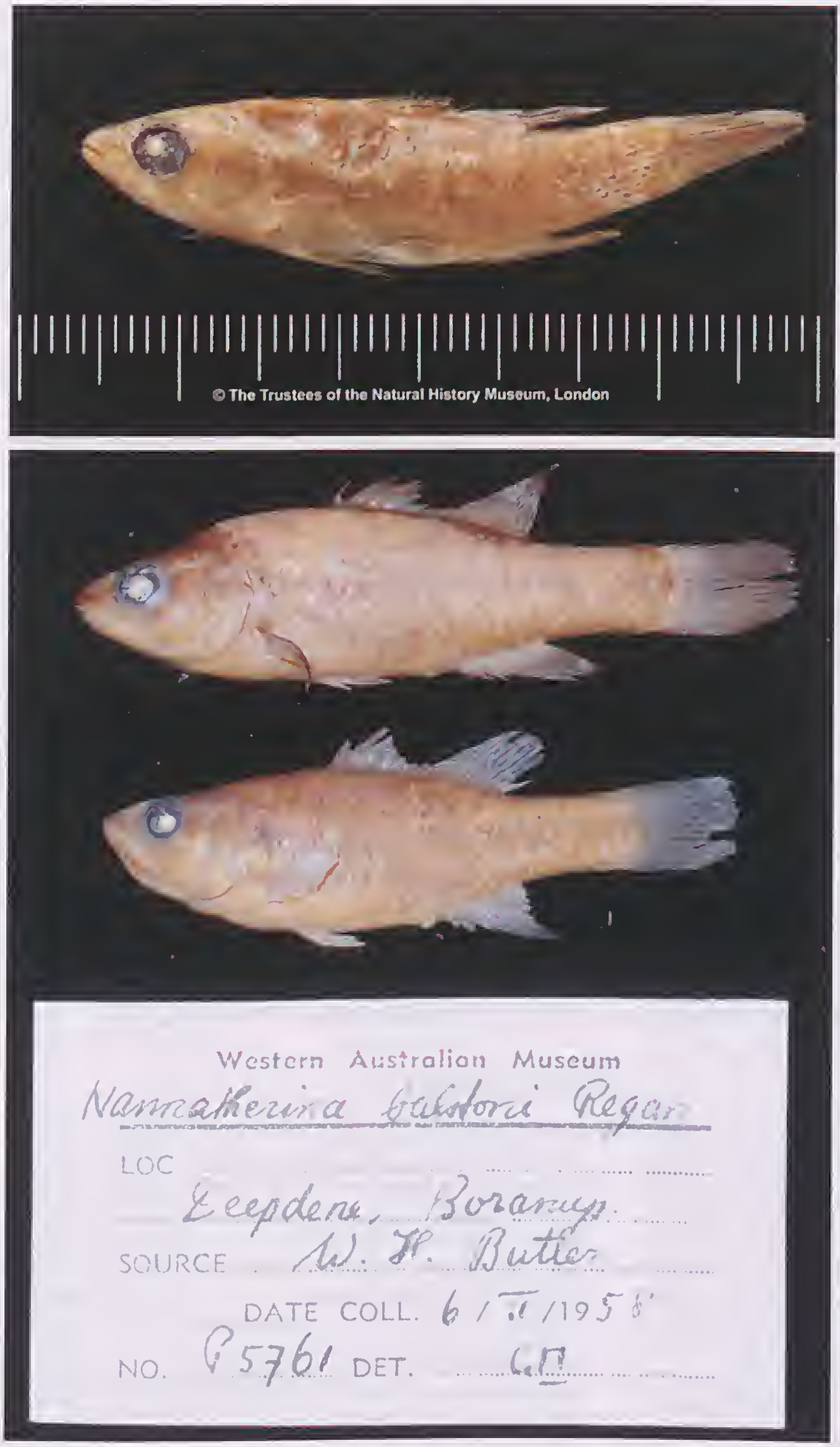
© The Trustees of the Natural History Museum, London
Western Australian Museum
Nannatherina balstoni Regan
LOC
Deepdene, Boranup.
SOURCE W. H. Butler
DATE COLL. 6 / II /1958
NO. P5761 DET. G.A.

Figure 1 (Above) The remaining syntype of *Nannatherina balstoni* from the King River (BMNH1906.11.1.21-21) (image provided by James Maclaine, British Museum of Natural History). (Below) Two specimens (WAM P.5761.001) of *N. balstoni* from Turner Brook collected in 1958 by W.H. Butler (photograph G. Moore).

in the upper Margaret River, one in the Gardner and Shannon rivers, and one that included fish from the Blackwood, Deep, Hay and Angove rivers. Using mtDNA, Murphy *et al.* (2010) demonstrated that, genetically, almost all populations of *N. balstoni* were significantly different to each other. Therefore, the loss of the Moore River, King River and Turner Brook populations has likely resulted in the irreversible loss of at least three genetically unique populations (see Figure 1). It is recommended that long term monitoring of populations across the range of the species is included in any recovery plan.

The mechanism for loss of *N. balstoni* from its type locality (King River) is unknown, but may be related to the presence of introduced species such as *Gambusia holbrooki* and/or *Oncorhynchus mykiss*, the latter of which was, until very recently, annually stocked into the river.

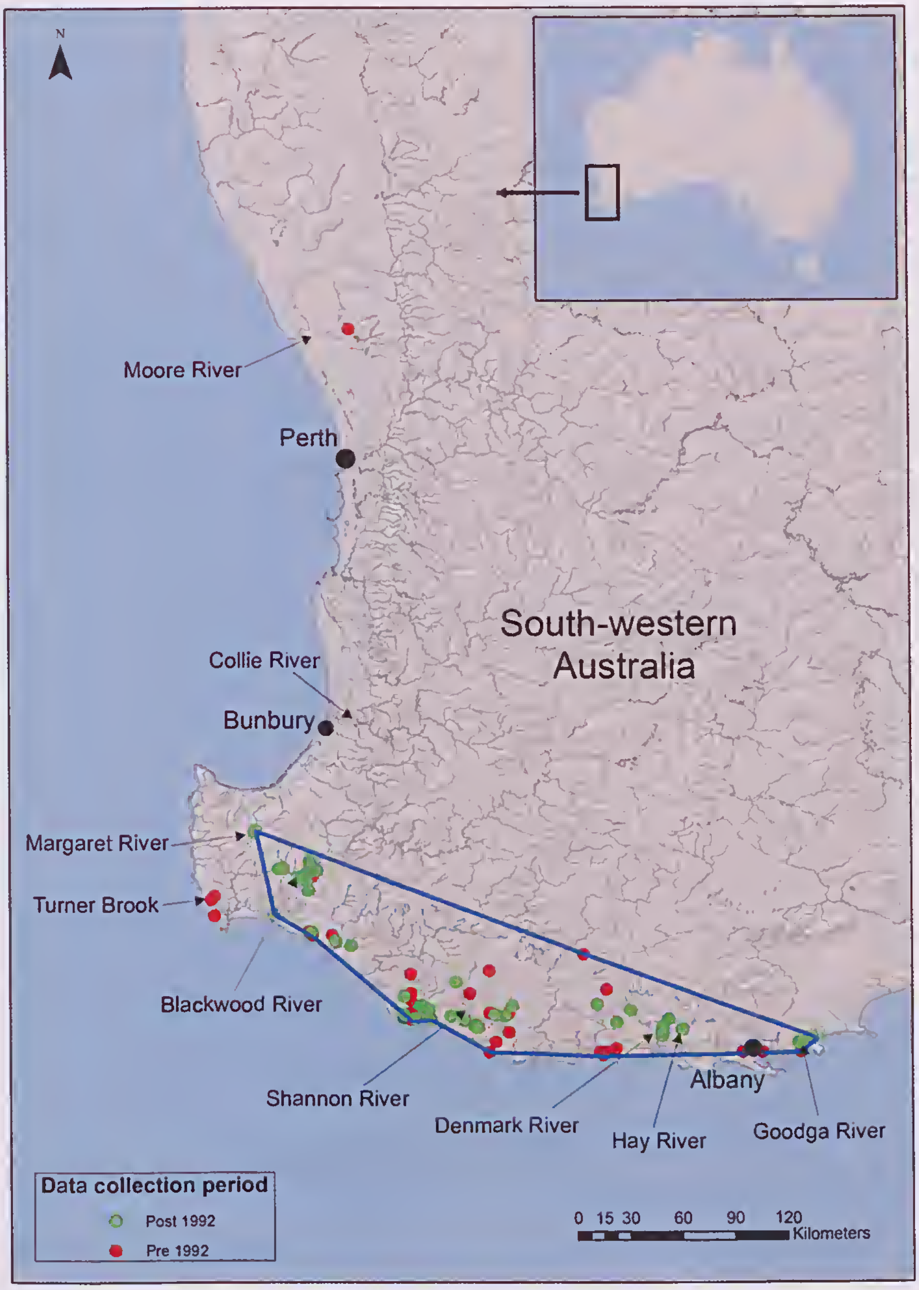

Figure 2 The known location points of *Nannatherina balstoni*. The current area of occupancy of *N. balstoni* is based on the distribution locations excluding the presumed extirpated populations in the Moore River and Turner Brook. These data are based on collections by the authors since 1992 and those deposited in various museums prior to 1992.

The only known *N. balstoni* specimens from the river are the two syntypes, one of which appears to have been lost. The second specimen is thus the sole remaining primary type specimen for the species (Figure 1) (BMNH1906.11.1.21-21).

Ground truthing data from the historical sites identified in the current study (Figure 1) is required in order to update the extant distribution and determine recent population trends. Such data will help guide management strategies for this species by identifying other populations that may have been lost and those populations that remain viable, as well as helping to formulate hypotheses surrounding the causes of the decline of *N. balstoni*. Any future recovery plans for the species should identify sites at risk from anthropogenic stressors and important refuge habitats. Such sites should be based on the re-examination of historically known populations and from the identification of populations that represent the most genetically significant units.

Management strategies, such as the designation of fish habitat protection areas (FHPA), public education including riparian landholders, and the quantification and mitigation of likely impacts on the species such as instream barriers, riparian zone degradation, and introduced fish species, are urgently required to abate the decline of this threatened, endemic species.

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Enhancing fish passage over large on-stream dams in south-western Australia: a case study

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Instream barriers are known to have major negative impacts on aquatic ecosystems; particularly on migratory fishes. These impacts include exclusion from critical habitats (particularly spawning habitats), reduced colonisation, genetic fragmentation, and increased rates of density dependent mortality below barriers. Construction of fishways can overcome many of the impacts of barriers on migratory fishes by providing passage over, through, or around artificial barriers. In south-western Australia, instream barriers are one of several major stressors on highly endemic (82%) freshwater fishes; many of which are potamodromous and migrate to spawn during the seasonal high flow period. Moreover, climate change has made the allocation of surface water more challenging due to a severe (~50%) reduction in surface flow over the past ~40 years. This study describes the design and construction of the largest fishway system built to date in this region and tests its functionality. The rock-ramp fishway system was located on Rushy Creek (an ephemeral tributary of the Blackwood River) and included a bypass and spillway fishway with an overall lift of 4.5 m. In spring 2010 and 2011, three of the eight native fishes (Western Minnow (*Galaxias occidentalis*), Western Pygmy Perch (*Nannoperca vittata*), and the Blue-spot Goby (*Pseudogobius olorum*)) in Rushy Creek were shown to pass upstream and downstream on the fishway system. Higher and more sustained flows in 2011 likely resulted in greater upstream fish passage in that year compared with 2010; highlighting the flow dependence of successful fish passage through fishways, which will have implications in terms of their functionality in drying climatic regions both in terms of changes in migration cues and fishway passage success. However, hydrological conditions during peak flow in both years also probably exceeded the swimming performance of the Western Pygmy Perch thereby preventing it negotiating the system during the early part of its spawning period, as opposed to the Western Minnow and the Blue-spot Goby both of which successfully negotiated the system during August and September. The findings highlight the importance of understanding species life-histories and swimming abilities, and have implications for future planning and design of fishways in this region to ensure they are appropriate for fish passage under future flow scenarios.

KEYWORDS: fish migration, rock-ramp fishway, swimming performance, surface flow decline, Galaxiidae, Percichthyidae, Gobiidae

INTRODUCTION

Artificial instream barriers such as dams can have severe and broad negative impacts on the structure and functioning of aquatic ecosystems (Bunn & Arthington 2002; Arthington 2012). Many fishes migrate within rivers as part of their life-cycle (often to access spawning habitats) and therefore the impact of instream barriers can be particularly severe on diadromous and potamodromous fishes (e.g. Lucas & Baras 2001; Gehrke *et al.* 2002; Gregory *et al.* 2002). The installation of fishways is a strategy aimed to enhance upstream passage of migratory fishes thereby at least partially overcoming one of the major ecological impacts of barriers. However, they have not always allowed complete passage of all species, particularly smaller-bodied fishes or those with poor swimming abilities (Katopodis & Aadland 2006). For example, in assessing the functionality of Victoria's existing fishways, just over half those assessed provided passage for greater than 70% of fish species (O'Brien *et al.* 2010).

Mediterranean climatic regions are typified by highly seasonal flow regimes due to strong seasonal rainfall patterns. Reductions in flow due to changing climate and water abstraction are recognised as a major threat to freshwater fishes, particularly in Mediterranean regions (Hermoso & Clavero 2011; Maceda-Veiga 2013). In Western Australia, surface water resources are most degraded in the south-west (Halse *et al.* 2002), primarily due to more concentrated human activity. Since the mid-1970s, a reduction of ~15% in annual rainfall and ~50% in surface flows has occurred in south-western Australia (Suppiah *et al.* 2007; Silberstein *et al.* 2012). Global climatic models project this drying trend to continue to 2030 with median rainfall and surface flow declines of ~8% and ~25%, respectively (Silberstein *et al.* 2012). This adds considerable pressure on managers to balance water extraction with environmental water requirements in the region such as ensuring adequate flows to sustain fish populations.

The relative depauperate (11 species) freshwater fish fauna of the region has the highest rate of endemism (82%) of any Australian drainage division (Allen *et al.* 2002; Morgan *et al.* 2011). These fishes have been particularly impacted by anthropogenic stressors, most notably riparian degradation, secondary salinisation (Morgan *et al.* 2003; Beatty *et al.* 2011), and introduced fish species (Morgan *et al.* 2004; Marr *et al.* 2010; Beatty & Morgan 2013). Most are known to undertake some form of migration as part of their life-cycle (Morgan 2003; Chapman *et al.* 2006; Beatty *et al.* 2010) with the numbers of fish migrating upstream positively related to the volume of peak flow discharge (Beatty *et al.* 2014). The combination of ongoing reductions in river flows due to climate change and physical impediments to spawning migration due to numerous instream barriers in the region is undoubtedly having a major impact on their lifecycles (Beatty *et al.* 2014).

Water allocation in Western Australia is administered under the *Rights in Water and Irrigation Act 1914* (RWIA), by the Department of Water, Government of Western Australia (DoW). Under the RWIA, surface water catchments may be proclaimed, which triggers the need for a surface water allocation plan. A key purpose for proclaiming catchments is to protect the water resource from overuse and prevent its degradation. When assessing proposed dams and any take of water the DoW is required to have regard to all matters listed in Schedule 1, clause 7(2) of the RWIA with the primary considerations in applying aquatic passage for a new dam including the flow period, duration of flow, seasonal movements of aquatic fauna, the presence of existing barriers on the tributary and connectivity of riparian vegetation. For example, the Whicher Area Surface Water Allocation Plan (WASWAP) includes a requirement to maintain passage of aquatic fauna through any proposed new dam located on a watercourse, where there is a known population or potential population of migratory aquatic fauna. The applicability of this condition is considered through an environmental assessment of the proposed dam location and the surrounding catchment (Department of Water 2009).

There is considerable literature on fishway design and species usage in eastern Australia (e.g. Mallen-Cooper 1999; Stuart & Mallen-Cooper 1999; Bice & Zampatti 2005; Mallen-Cooper & Brand 2007; Stuart *et al.* 2008; O'Brien *et al.* 2010). However, while the majority of south-western Australian fishes are endemic and are almost exclusively small bodied (i.e. <200 mm total length) (Allen *et al.* 2002; Morgan *et al.* 2011), the applicability of the existing information on fishways designed for eastern Australian fishes to south-west Western Australian species has not been properly assessed (Morgan & Beatty 2006). Moreover, despite barriers representing a major threat to fishes in this region, fishway construction in Western Australia is still in its infancy compared with the eastern states of Australia with most (six of seven fishways) being constructed in the last 12 years for barriers with relatively low lifts (< 2 m) with mixed levels of operating success, and galaxiids found to be the dominant users (Morgan & Beatty 2004 a, b; Morgan & Beatty 2006; Beatty *et al.* 2007).

Fishway design in this region has also been hampered by the lack of information pertaining to the swimming performance of any of the native freshwater fishes. Understanding swimming performance of fishes (including prolonged, sustained and burst swimming performance) is paramount for predicting their ability to negotiate instream barriers (e.g. Starrs *et al.* 2011). Only recently has work begun on determining these swimming performance metrics that will be extremely valuable in designing more effective fishways to facilitate the passage of a larger proportion of native fish species past barriers (Keleher 2011).

Amelioration of larger barriers (>2 m) has not previously been undertaken in Western Australia. Moreover, the efficiency of these fishways has not been assessed in relation to the recently quantified swimming performances of native and introduced fishes. Gathering such hydro-ecological information is of paramount importance to help refine the design of fishways in this region; particularly under the influence of a drying climate.

The current study aimed to describe the design, installation and operational success of by far the largest fishway system yet constructed in south-western Australia and the first constructed under prescription from a surface water allocation plan. Temporal patterns of fish use of the fishway were quantified during the major flow and peak migratory period of several species over two consecutive years. It is hypothesised that fish passage success will be related to the hydrology on the fishway system.

MATERIALS AND METHODS

Study site and resident fish fauna

Rushy Creek is an ephemeral tributary of the lower Blackwood River, the largest river by discharge in south-west Western Australia (Figure 1). Rushy Creek is approximately 44 km long and has a rain catchment of 22 km^2. While there are a number of on-stream soaks and dams, the majority of these are small and would not pose significant barriers to fish migration during winter and spring. There are four relatively large dams, but their location in the upper reaches has limited impact on connectivity throughout most of the catchment.

A fish survey was undertaken in December 2007 (Beatty *et al.* 2008a) in the McLeod Creek catchment, including two sites in Rushy Creek. Four native estuarine species (South-western Goby (*Afurcagobius suppositus*), Blue-spot Goby (*Pseudogobius olorum*), Western Hardyhead (*Leptatherina wallacei*) and Black Bream (*Acanthopagrus butcheri*)), four native freshwater species (Western Minnow (*Galaxias occidentalis*), Western Mud Minnow (*Galaxiella munda*), Nightfish (*Bostockia porosa*) and Western Pygmy Perch (*Nannoperca vittata*)), and one introduced species (Eastern Gambusia (*Gambusia holbrooki*)) were identified in the survey. Rushy Creek was shown to house all of those native freshwater fishes (aside from *G. munda*) that were in the McLeod system, along with one estuarine species (i.e., South-western Goby), and the introduced species (i.e., Eastern Gambusia) (Beatty *et al.* 2008a). As most of the native freshwater species recorded in the Rushy Creek system are known to undertake spawning migrations (Beatty *et al.* 2014), it was concluded that they would likely be impacted by major instream barriers.

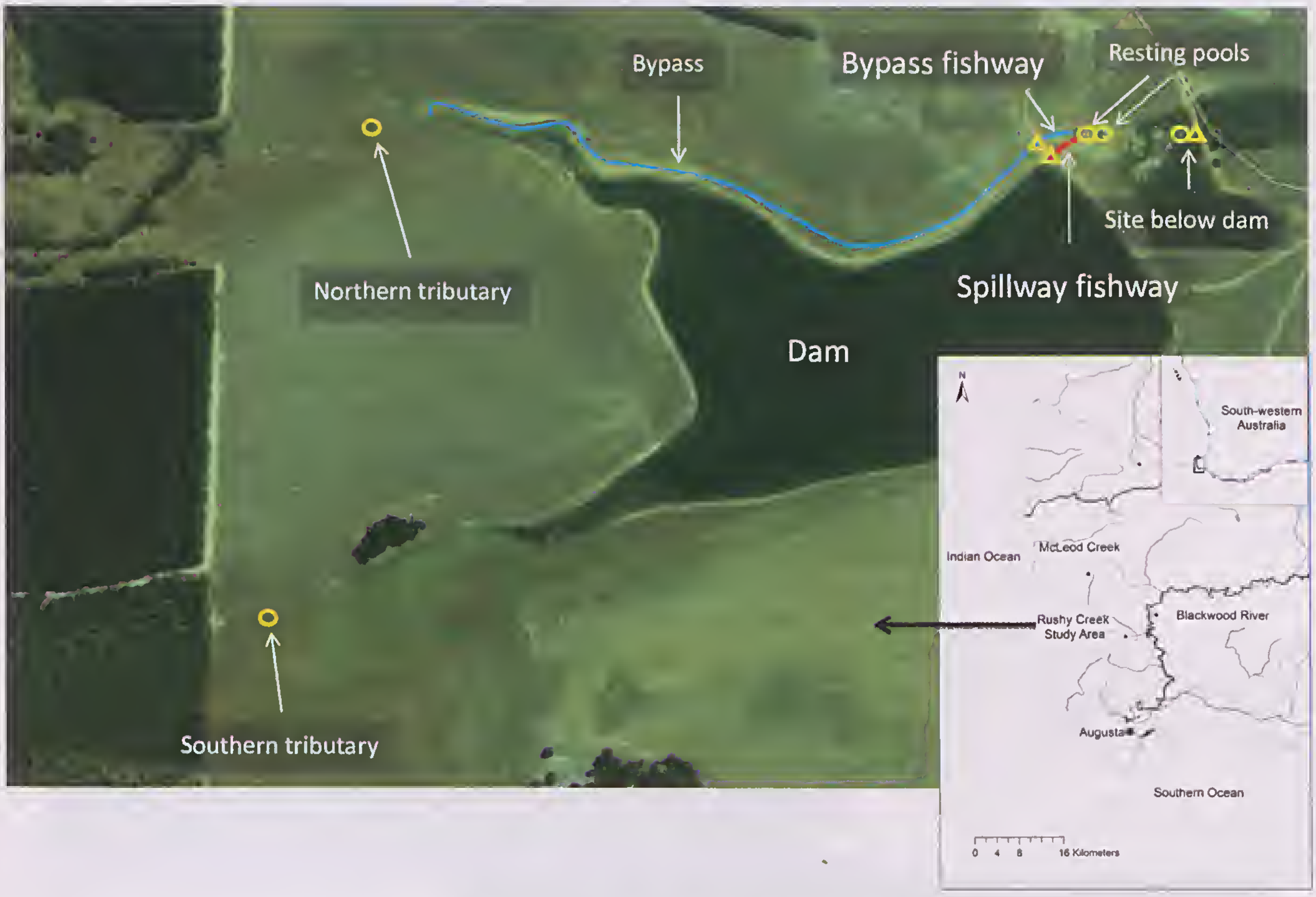

Figure 1 Location of Rushy Creek, south-western Australia. The aerial photo shows the location of the Rushy Creek Dam and the bypass and spillway fishways along with other key habitats that were sampled as part of the current study. N.B. blue line indicates the passage of the bypass around the Dam, the yellow triangles indicate fyke netting sampling sites and the yellow circles indicate those sites sampled for densities.

Design and construction of the fish passage system

In 2008, through the WASWAP, a condition to provide aquatic passage was placed on an application for a proposed dam located in the lower reaches of Rushy Creek; 0.5 km upstream of the confluence with McLeod Creek and 1.8 km upstream of the confluence with the Blackwood River (Figure 1). The proposed reservoir was to intercept three tributaries of the Rushy Creek system, two entering the reservoir from the south and one from the north. Its location would therefore stop any upstream migration into Rushy Creek and impact on the recruitment and reduce the availability of habitat for freshwater species (i.e., ~42 km upstream).

As several fish species were known from Rushy Creek, a range of possible migration periods had to be considered. Being an ephemeral tributary, this required ensuring that early and late low flow events were able to bypass the reservoir. Therefore, a condition was applied that would result in the creation of an open-channel, low-flow bypass connecting the aquatic passage system with the northern tributary upstream of the reservoir; which comprised ~63% of both the stream length (27.7 km) and catchment area (13.7 km^2) of Rushy Creek.

Design and installation of the low flow bypass and fish passage systems was the responsibility of the proponent, however, the DoW provided advice and outlined key design criteria. The cost of a vertical slot system for the 4.5 m lift required was deemed unacceptable at the time and as rock-ramp systems were known to be successful in facilitating the passage of a range of small fish species in eastern Australia (O'Brien *et al.* 2010) and to a lesser extent in south-western Australia (Morgan & Beatty 2004a, b; 2005; Beatty *et al.* 2007), a rock-ramp fish passage system was proposed as the most cost effective option.

The original concept comprised diverting low flows from the northern tributary into an open channel constructed along the northern edge of the reservoir. At the spillway a rock-ramp system would then enable the water from both the open channel and reservoir to discharge into a resting/stilling pool. In low flow conditions the water would continue down a rock-ramp system into a second resting pool at the base of the spillway on the original stream. The advised criteria for the rock-ramps were the commonly adopted specifications of a maximum overall slope of 1:20 comprising 100 mm steps at 2 m intervals (Thorncraft & Marsden 2000). Inclusion of resting pools was also advised, in accordance with literature that recommended a series of rock-ramps with resting pools be used for larger lifts (Water and Rivers Commission 2002; Kapitzke 2010).

During construction in 2009, contractor delays led to complications, and emergency works on the spillway were required during significant high flow periods. This resulted in a spillway and fish passage configuration that deviated from the recommended design criteria. The final spillway configuration comprised two major resting pools connected by cascade rock-ramps (Figure 2). The ramps varied in length from 10 to 30 m with overall slopes varying from 1:10 to 1:66, resulting in individual lifts of up to 2.5 m. The top ramp comprised a cascade connecting to the spillway crest and a separate channel connecting to the bypass system, both of these had an overall slope of 1:11 but the separate channel also included a sequence of significant steps (100, 290 and 340 mm) within a 3 m length. Being a confined and steep channel, these steps do not drown out in higher flows (Figure 2).

The final structure was further complicated due to its connection to an old soak adjacent to the stream rather than the stream itself. Water from the spillway entered the soak and overflowed the downstream clay bund that created a 400 mm step at the bottom of the system (Figure 2). This step partially drowned out in higher flows providing alternative paths for fish movements. Documented specifications for cascade rock-ramp

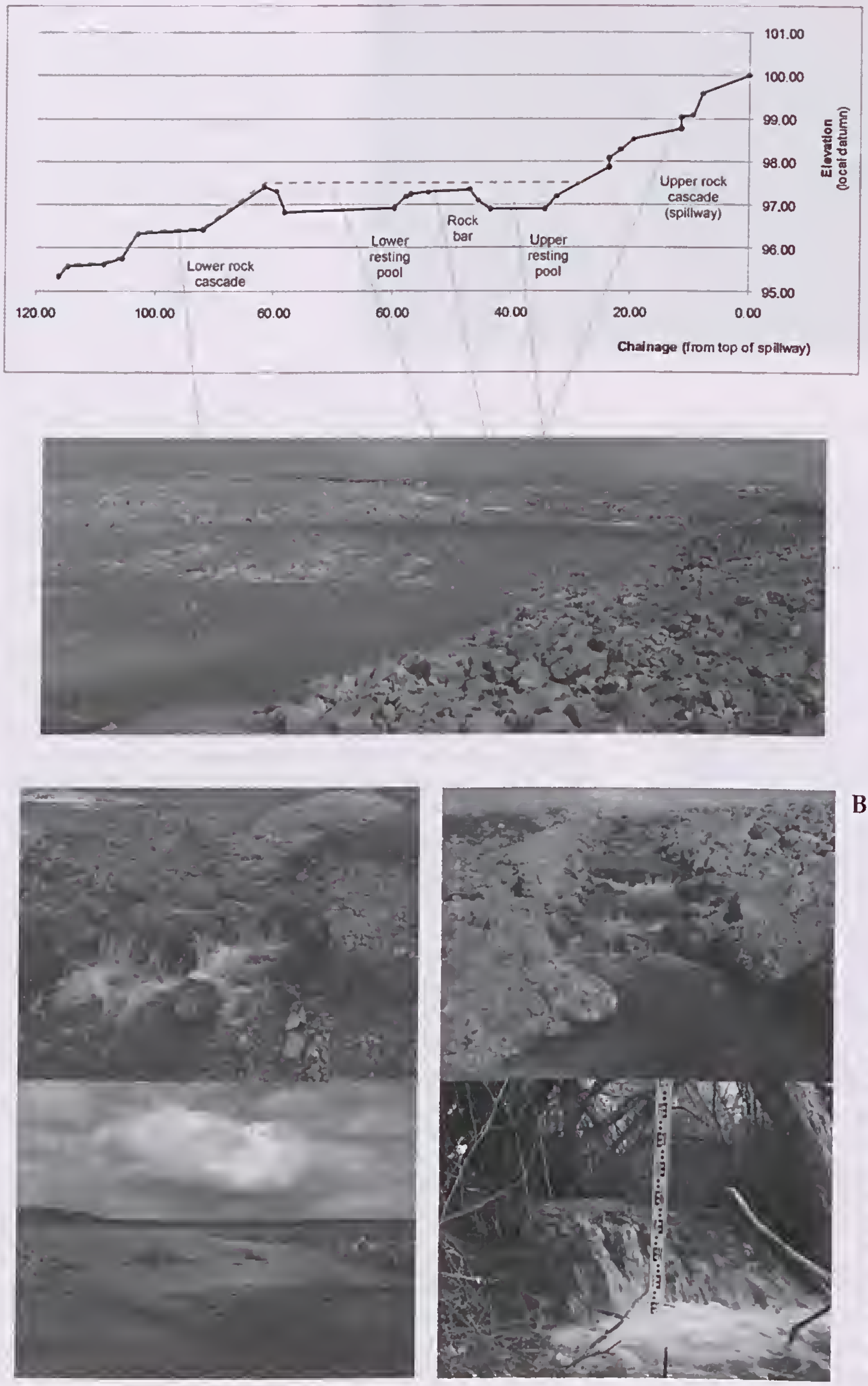

Figure 2 A) Cross sectional profile and image of the spillway fishway identifying the rock cascades, bar and resting pools. B) (Clockwise from top left) significant steps located at the top (left image) and bottom (right image) of the bypass fishway, significant step located downstream of the spillway where water spills over the clay bund wall of the soak before entering the original stream, fyke nets established to monitor up and downstream movements on the spillway.

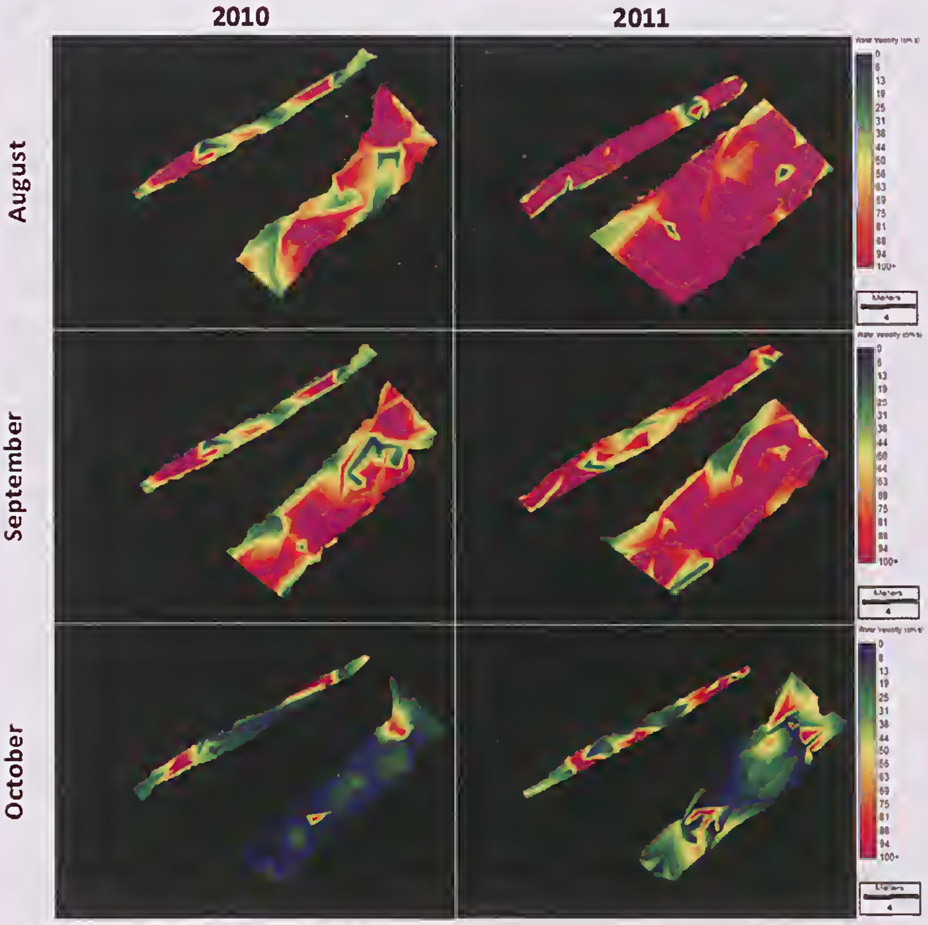

Figure 3 The flow profiles of the bypass (left) and spillway (right) fishways in August (top), September (middle) and October (bottom) 2010 and 2011. N.B. the clear reductions in flow rates between the sampling months in each year and the greater area of low flow on the spillway compared to the bypass in October.

systems suggest an overall slope of 1:9 and maximum lift per cascade of 0.4 m (Kapitzke 2010). These specifications were therefore exceeded in the system that was constructed. To assess the functionality of the fishway system, fish movement and density surveys were undertaken between late winter and early spring in both 2010 and 2011.

Assessing fish passage

A total of six monthly sampling events were undertaken in August, September and October 2010 and 2011 during the major high flow period of rivers in this region. An assessment of the upstream and downstream movement patterns of fishes and their ability to traverse the two fishways was made in each month. On each sampling occasion, fyke nets (11.2 m in total width, consisting of two 5 m wings and a 1.2 m wide mouth fishing to a depth of 0.8 m, 5 m long pocket with two funnels all comprised of 2 mm woven mesh) were set facing upstream and downstream above both the bypass fishway and the spillway fishway (Figure 1). Fyke nets were checked every 24 hrs for three consecutive 24 hr periods during each sampling month. In order to compare species movements in the unimpeded section of Rushy Creek downstream of the dam with those on the fishways, a downstream site in Rushy Creek was also monitored for upstream movements in 2011 (Figure 1). The latter downstream site was monitored following the fyke netting on the fishways in each month so as not to bias the captures on the fishways. Prior to the fyke nets being set on the fishways in 2011, resident fish (that would otherwise bias the fishway catch) were removed from shallow water habitats (<~20 cm maximum depth) of both the spillway crest and bypass using a back-pack electrofisher (Smith Root Model LR20). This was undertaken as the fyke nets were unable to be set precisely at the upstream end of the fishway structures due to lack of depth and excessive flow.

All fishes captured were identified and measured to the nearest 1 mm total length (TL), and evidence of spawning activity recorded in larger (>60 mm TL) Western Minnow (i.e. obvious presence of eggs or exudence of sperm), before being released. Captures on the spillway and in the Creek downstream of the fishway system were scaled to 100% as the fyke nets did not permit the channel to be fully blocked (~90% and 60% blockage for the spillway and Rushy Creek, respectively).

Mean upstream and downstream movement was determined for each species in each month at each site. Spatial and temporal patterns of species densities were determined on each monthly sampling period in the stream below the resting pools, in the resting pools, and the streamlines upstream of the dam and bypass channel. Density sampling was undertaken upon cessation of fyke net sampling each month using a combination of replicate seine netting (10 m seine, 2 mm mesh width) in the spillway resting pools and a back-pack electrofisher at the other sites. Three replicate samples for each technique were taken from randomly chosen stream habitats within each location and all fish captured were identified and measured to the nearest 1 mm TL, and mean density of fish (fish.m^{-2}) was determined for each species, at each site, in each sampling month. Temperature, pH, salinity, conductivity and dissolved oxygen were measured at three sites in Rushy Creek on each sampling month and a mean (±1S.E.) calculated.

Flow modelling

Depth-flow profiling was undertaken on the bypass fishway, spillway fishway, and riffle sections downstream of the fishway to characterise the hydrological conditions present on the fishway system during each sampling occasion. Depth and velocity measurements were made (flow measured with Global Water FP101 and Hontzsch HFA probes, and channel widths measured using Bosch DLE 70) at up to 15 points along transects positioned perpendicular (i.e. cross section) or parallel (i.e. longitudinal section) to the flow. Depth-flow profiling was also undertaken on the two largest steps located near the top and bottom of the bypass fishway with three measurements being taken during each sampling period.

Hydraulic modelling to describe flow characteristics in each area in each month sampled was undertaken using the program IDRISI Taiga. This allowed comparison of flow characteristics against laboratory derived swimming performance metrics (Keleher 2011). Flow data was entered into the program IDRISI Taiga as vector points. Interpolations between vector points were then created using the TIN (triangulated irregular network) model to generate a triangulated irregular network model. The TIN first divides the set of input data points into sections, and then each section is triangulated. The resulting 'mini-TINs' are then merged and a local optimisation routine is run during the merge process to ensure that Delaunay criteria are met in the final TIN (i.e., ensures that maximisation of the minimum angles of all of the triangles contained within the final triangulation occurs). The previous TIN images were reclassified and the pixel values were stored in each image. This process resulted in composite flow profiles being generated of the bypass and spillway fishways on each sampling occasion. The RECLASS module was also used to determine the percentage of area on the fishway and bypass greater or less than 65 cm.sec^{-1} (i.e. the U_{sprint} value (Starrs *et al.* 2011) of the Western Pygmy Perch determined by Keleher (2011)).

Statistical analysis

Differences in the mean upstream and downstream passage among the three species that utilised the fishways (i.e. Western Minnow, Western Pygmy Perch and the Blue-spot Goby; see results), between the bypass and spillway fishways, and between years sampled were tested using a full factorial general linear model, where: $N_{movement} = \mu + S_i + F_j + Y_k + S_ixF_j + S_ixY_k + F_jxY_k + S_ixF_jxY_k + e$, where μ is the overall average upstream or downstream fish movement of fish through the fishway system, S_i the fixed effect of the ith species, F_j the fixed effect of the jth fishway, Y_k the fixed effect of the $_k$th year, and S_ixF_j, S_ixY_k, F_jxY_k, $S_ixF_jxY_k$ are the various interactions between the factors, and e the residual error. All data were log+1 transformed prior to analysis and tests were undertaken in the SPSS (v21) statistical program.

RESULTS

Environmental variables and flow profiles

Water quality in Rushy Creek was fresh (<650 μS.cm^{-1}), highly oxygenated (>92 % DO), and near neutral (pH 6.9-7.8) throughout the sampling period (Table 1). There was a considerably greater average water velocity on both the bypass and spillway fishways in all months sampled in 2011 compared with 2010. The increase in velocities between 2010 and 2011 was proportionally greatest on the bypass in August (70% increase) and September (82% increase) compared to the spillway in those months (55 and 16% increase, respectively) (Table 2). Average flow velocities were greater on the spillway compared to the bypass in August and September in both 2010 and 2011, but were greater on the bypass compared to the spillway in October of both years (Table 2).

The composite spatial flow profiles of the two fishways revealed that both the bypass and spillway fishways were dominated by areas of high flow (>65 cm.sec^{-1}) in August and September in both years.

Table 1 Mean (±1S.E.) physicochemical variables in Rushy Creek in the months sampled in 2010 and 2011.

Year	Month	Temp. (° C)	pH	Cond. (μS.cm^{-1})	NaCl (ppm)	TDS (ppm)	DO (mg.l^{-1})	DO (%)
2010	August	11.3 (0.03)	6.93 (0.04)	532.6 (4.56)	155.6 (0.13)	84.6 (0.07)	10.4 (0.14)	92.2 (2.69)
	September	14.5 (0.12)	6.90 (0.07)	535.3 (3.28)	157.3 (1.01)	99.76 (0.68)	9.49 (0.06)	93.1 (0.09)
	October	18.23 (0.09)	7.38 (0.08)	647.7 (18.31)	186.4 (4.18)	145.2 (4.82)	9.79 (0.10)	101.1 (1.23)
2011	August	14.9 (0.07)	–	252.9 (0.59)	126.8 (0.19)	121.0 (1.03)	9.9 (0.04)	98.7 (0.47)
	September	15.9 (0.1)	7.8 (0)	233.1 (0.15)	116.3 (0.2)	111.2 (0.85)	9.4 (0.04)	92.5 (0.43)
	October	23.3 (0.09)	7.4 (0.06)	186.8 (0.07)	93.4 (0.13)	91.2 (0.07)	8.5 (0.15)	101.9 (0.87)

Table 2 Mean (±1S.E.) water velocity (cm.sec^{-1}) on the bypass and spillway fishways on Rushy Creek in each month sampled in 2010 and 2011.

	Bypass (cm.sec^{-1})		**Spillway (cm.sec^{-1})**	
	2010	**2011**	**2010**	**2011**
August	55.23 (6.02)	93.77 (9.54)	62.57 (6.04)	96.89 (7.74)
September	37.83 (4.08)	68.86 (6.81)	60.95 (4.78)	70.50 (4.84)
October	23.16 (2.88)	31.10 (3.35)	12.64 (1.64)	23.33 (2.29)

Table 3 The percentage (%) of the total wetted area on the bypass and spillway fishways on Rushy Creek that had water velocities < 65 cm.sec^{-1} (i.e. below the U_{sprint} value of the Western Pygmy Perch (Keleher 2011)) in each month sampled in 2010 and 2011.

	Bypass (% of area <65 cm.s^{-1})		**Spillway (% of area <65 cm.s^{-1})**	
Month	**2010**	**2011**	**2010**	**2011**
August	71.51	18.36	40.50	11.19
September	68.98	36.01	48.17	23.76
October	84.86	71.55	96.14	94.44

There was a larger reduction in flow rates between September and October on the spillway compared to the bypass in both years with ~96% and ~94% of the spillway area having a velocity <65 cm.sec^{-1} in October 2010 and 2011, respectively, compared with ~85% and ~72% of the bypass during those corresponding months (Table 3, Figure 3). This was also reflected in the average velocity on the spillway being less than that on the bypass in October in 2010 and 2011 (Table 2).

Overall captures and fishway utilisation

A total of seven and nine fish species were recorded during 2010 and 2011, respectively (Tables 4 and 5; Figures 4 and 5). In 2010, a total of 1760 individual fish were recorded of which 533 (30.3%) were captured on the bypass and 1227 (69.7%) on the spillway. In 2011, a total of 4183 fish were recorded utilising the fishways (a 138% increase from 2010). Of these 2275 (54.4%) were captured on the bypass and 1908 (45.6%) on the spillway. The Western Minnow and Western Pygmy Perch dominated captures on the fishways in both years with the native Blue-spot Goby also captured on the spillway (Figures 5–7). There was a significant effect of species (F = 29.191, p = 0.00), fishway (F = 14.038, p = 0.001), and

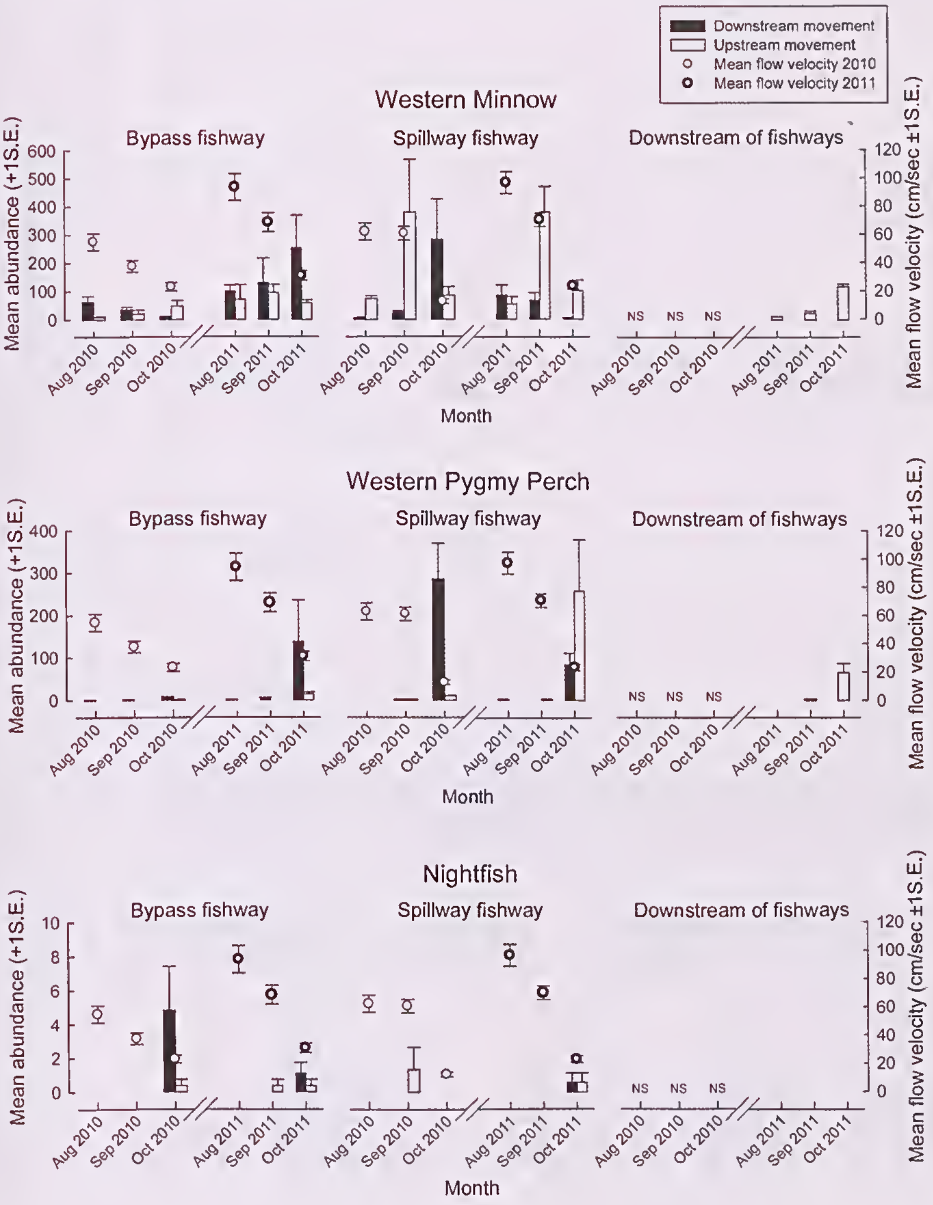

Figure 4 Mean (+1 S.E.) upstream and downstream movement of Western Minnow, Western Pygmy Perch and Nightfish recorded on the bypass fishway, spillway fishway and in Rushy Creek downstream of the dam (upstream movement only in 2011) during each sampling month in 2010 and 2011.

Table 4 Species densities (fish.m^{-2}) at the sites sampled in 2010 in the Rushy Creek system. N.B. A = August, S = September, O = October, ±1 S.E. in parentheses.

	Native freshwater fishes				Native estuarine fishes			Introduced fishes		Freshwater crayfish		
Site	Western Pygmy Perch	Western Minnow	Nightfish	Freshwater Cobbler	Blue-spot Goby	South-western Goby	Western Hardyhead	Eastern Gambusia	Goldfish	Marron	Gilgie	Yabby
Rushy Creek below fishways	A=0.39 (0.19) S=1.30 (0.2) O=0.17 (0.17)	A=0.35 (0.15) S=1.53 (1.16) O=0.66 (0.29)	O=0.03 (0.03)		A=0.01 (0.01) S=0.03 (0.03) O=0.02 (0.02)	A=0.05 (0.03) S=0.42 (0.16)		A=0.13 (0.13) S=0.33 (0.26) O=0.17 (0.08)		S=0.01 (0.01)		S=0.02 (0.02)
Lower resting pools	S=0.02 (0.02) O=0.07 (0.04)	A=1.63 (0.35) S=2.56 (1.07) O=5.33 (1.78)								S=0.02 (0.02)		
Upper resting pool	O=0.31 (0.28)	A= 3.13 (2.94) S=3.6 (3.2) O= 12.6 (9.82)			O=0.04 (0.04)			O=0.56 (0.56)		A=0.01 (0.01)	O=0.02 (0.02)	
Northern tributary above fishway: farmland	A=0.04 (0.02) S=0.01 (0) O=0.01 (0.01)	A=0.08 (0.03) S=0.25 (0.1) O=0.16 (0.07)	S=0.01 (0.01)					S=0.01 (0.01) O=0.01 (0.01)				A=0.02 (0.01) S=0.03 (0.01) O=0.25 (0.03)

Table 5 Species densities (fish.m^{-2}) at the sites sampled in 2011 in the Rushy Creek system. N.B. A = August, S = September, O = October, ±1 S.E. in parentheses.

	Native freshwater fishes				Native estuarine fishes			Introduced fishes		Freshwater crayfish		
Site	Western Pygmy Perch	Western Minnow	Nightfish	Freshwater Cobbler	Blue-spot Goby	South-western Goby	Western Hardyhead	Eastern Gambusia	Goldfish	Marron	Gilgie	Yabby
Rushy Creek below fishways	A=0.8 (0.24) S=0.59 (0.12) O=1.2 (0.65)	A=1.47 (0.79) S=1.84 (1.32) O=0.26 (0.17)	A=0.16 (0.13) O=0.03 (0.03)	S=0.04 (0.04) O=0.03 (0.03)	A=0.32 (0.18) S=0.44 (0.26) O=0.52 (0.23)	S=0.56 (0.29)	A=0.1 (0.1) S=0.03 (0.03)	A=0.58 (0.43) S=0.74 (0.74) O=3.33 (2.4)	A=0.12 (0.06)			A=0.03 (0.03) S=0.12 (0.07) O=0.45 (0.38)
Lower resting pools	A=0.02 (0.02) S=0.16 (0.07) O=3 (1.26)	A=0.72 (0.28) S=1.85 (0.7) O=3.42 (1.85)		S=0.01 (0.01)	S=0.18 (0.05) O=0.14 (0.1)			A=0.4 (0.3)				
Upper resting pool	A=0.02 (0.02) S=0.25 (0.11) O=0.22 (0.22)	A=2.3 (0.8) S=3.2 (1.31) O=5.5 (4.21)			A=0.01 (0.01) S=0.52 (0.2) O=0.21 (0.21)			S=0.02 (0.02)				O=0.02 (0.02)
Upstream crest of spillway	O=0.09	A=0.01 O=0.09			A=0.06 S=0.08 O=0.19			S=0.05				A=0.03 S=0.01 O=0.03
Upstream crest of bypass	O=0.55	O=0.25	O=0.05		A=0.04						S=0.04	A=0.04
Northern tributary above fishway: farmland	A=0.2 (0.08) S=0.06 (0.03) O=2.98 (2.65)	A=0.05 (0.03) S=0.14 (0.02) O=1.72 (0.84)	A=0.01 (0.01) S=0.02 (0.02) O=0.08 (0.01)							N=0.01 (0.01)	A=0.02 (0.01) O=0.06 (0.02)	A=0.06 (0.01) S=0.08 (0.01) O=0.07 (0.05)
Southern tributary above fishway: bushland		S=0.07 (0.07) O=0.17 (0.17)									S=0.21 (0.1) O=0.26 (0.08)	S=0.02 (0.02) O=0.04 (0.04)
Southern tributary above fishway: farmland	S=0.06 (0.02) O=2.97 (2.52)	A=1.01 (0.75) S=0.51 (0.34) O=0.44 (0.28)	O=0.01 (0.01)		A=0.1 (0.03) S=0.07 (0.01) O=0.09 (0.06)			A=0.01 (0.01)			A=0.01 (0.01) S=0.01 (0.01) O=0.09 (0.04)	A=0.14 (0.07) S=0.02 (0.01) O=0.11 (0.06)

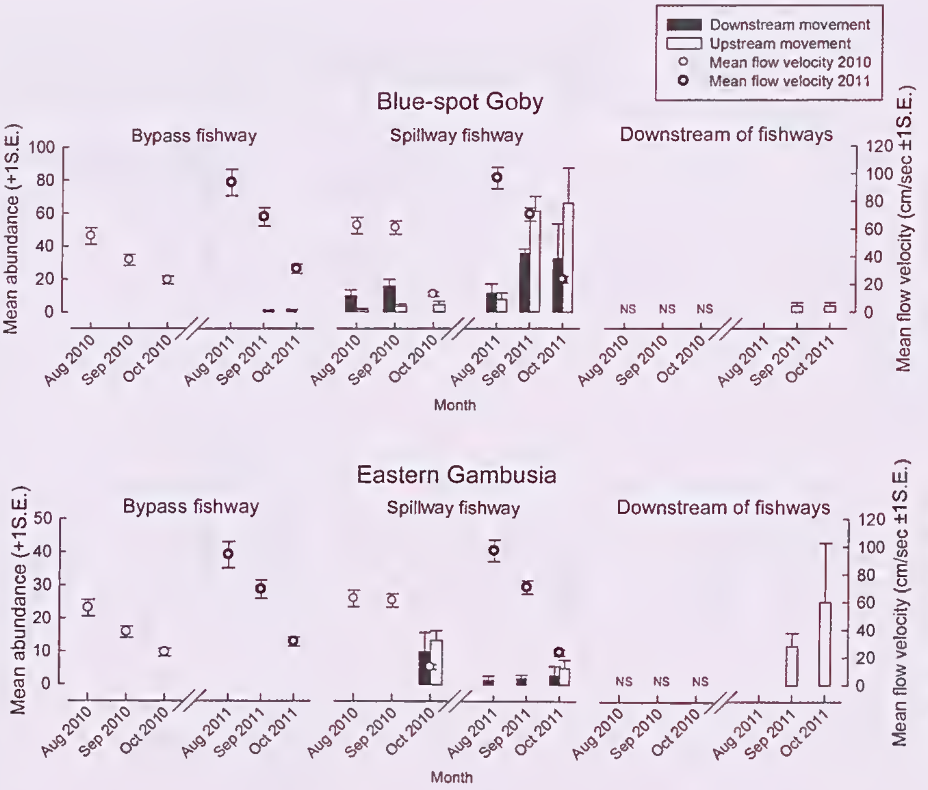

Figure 5 Mean (+1 S.E.) upstream and downstream movement of the Blue-spot Goby and introduced Eastern Gambusia recorded on the bypass fishway and spillway fishway, and in Rushy Creek downstream of the dam (upstream movement only in 2011) on Rushy Creek during each sampling month in 2010 and 2011.

year (F = 4.88, p = 0.037) but none of the possible interactions between the factors on the mean numbers of fish moving upstream over the fishway system. There was a significant effect of species (F = 9.380, p = 0.01) but not fishway (F = 2.133, p = 0.157), year (F = 1.14, p = 0.296) nor any interactions between the factors on the mean numbers of fish moving downstream over the fishway system.

In 2010 in the bypass channel, 213 (40.0%) fish were moving upstream and 320 (60.0%) downstream. All upstream captures in the bypass channel were freshwater endemic fishes comprising 210 (98.6% of total) Western Minnows, two (0.9%) Western Pygmy Perch and one (0.5%) Nightfish (Figure 4). On the spillway in 2010, 1003 (81.7%) fishes were moving upstream and 224 (18.3%) downstream. Upstream captures of fishes comprised 928 (92.5%) Western Minnows, 23 (2.2%) Western Pygmy Perch, 18 (1.8%) Blue-spot Gobies, 2 (0.2%) Nightfish, and the introduced Eastern Gambusia 32 (3.2%).

Downstream movement in the bypass in 2010 consisted of 285 (89.1%) Western Minnows, 21 (6.6%) Western Pygmy Perch, 13 (4.1%) Nightfish, and a single Western Mud Minnow. Downstream movement on the spillway consisted of 119 (53.1%) Western Minnows, 76 (33.9%) Western Pygmy Perch, 26 (11.6%) Blue-spot Gobies, and 3 (1.3%) Eastern Gambusia (Figure 5).

In 2011 in the bypass channel 575 (25.6%) fish were moving upstream and 1700 (74.7 %) downstream. Of the upstream moving captures, 533 (92.7%) were Western Minnows, and 38 (6.6%) were Western Pygmy Perch (Figure 4). On the spillway moving upstream, 765 (55.3%) Western Minnows were captured, 400 (28.9%) Western Pygmy Perch, and 211 (15.3%) Blue-spot Gobies (Figures 4 and 5). There was therefore an increase in the proportion of Western Pygmy Perch moving upstream over the bypass from 2.2% in 2010 to 28.9% in 2011. Similarly, an increase in the proportion of Blue-spot Goby moving upstream on the spillway occurred between 2010 (1.8%) and 2011 (15.2%).

Downstream captures on the bypass in 2011 consisted mostly of the Western Minnow (1311, 77.1%) and Western Pygmy Perch (384, 22.6%). There was therefore an increase in the proportion of Western Pygmy Perch moving downstream over the bypass from the 6.6% recorded in 2010. There was also a reduction in the proportion of Nightfish moving downstream from the 4.1% in 2010 to just 0.2% in 2011 (Figure 4). Downstream movements on the spillway in 2011 largely consisted of the Western Minnow (272, 51.9%), Western Pygmy Perch (113, 21.6%), and Blue-spot Goby (127, 24.2%) (Figures 4 and 5).

Expansion of the fyke netting program in 2011 to include a site on Rushy Creek below the dam resulted in the recording of the Freshwater Cobbler (*Tandanus bostocki*) that was not recorded during the density estimate sampling. The introduced Goldfish (*Carassius auratus*) was also recorded below the dam in 2011 and had not been previously recorded in McLeod or Rushy Creek. The Freshwater Cobbler and Western Mud Minnow (the latter recorded in 2010), were not recorded on either the bypass or spillway, or either branch of Rushy Creek in 2011.

Spatial and temporal patterns in movements and population structures

Upstream passage of the Western Minnow was recorded on the bypass and spillway fishways in all months in both years (Figure 4). There was a clear peak in upstream

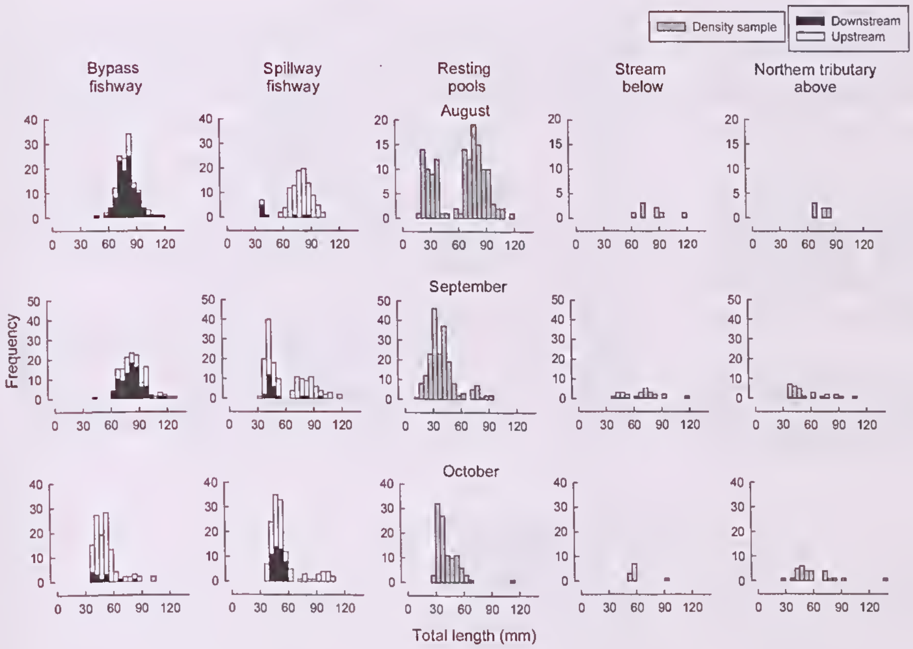

Figure 6 Length-frequency distributions of the Western Minnow in Rushy Creek at the sites and months sampled in 2010.

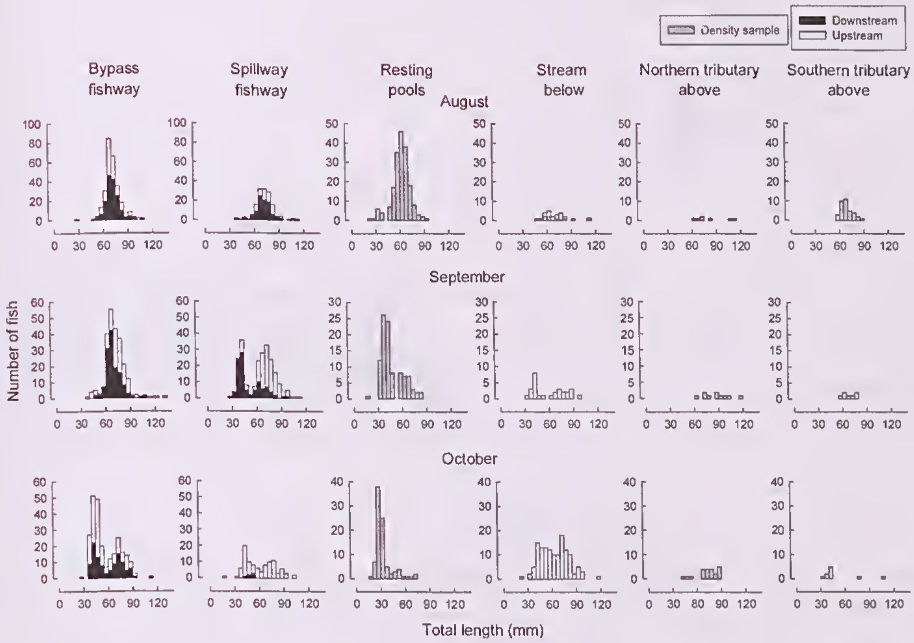

Figure 7 Length-frequency distributions of the Western Minnow in Rushy Creek at the sites and months sampled in 2011.

movement on the spillway fishway in September in each year with a less distinct peak occurring on the bypass in October and September in 2010 and 2011, respectively (Figure 4). Upstream movement of the species was recorded below the dam during all months sampled in 2011 peaking in October (Figure 4). Downstream passage of the species also occurred in all months on both fishways in both years. On the spillway fishway, a clear peak in downstream movement occurred in October 2010 *cf* a decline in movement occurring in that month in 2011 (Figure 4). On the bypass, a gradual decline in downstream movement occurred monthly in 2010 with the opposite trend occurring in 2011 (Figure 4).

Length frequency distributions of the Western Minnow in 2010 and 2011 confirmed the population was self-maintaining with multiple size cohorts being present in all months (that would likely correspond to age cohorts) (Figures 6 and 7). The length-frequency distributions in the resting pools were generally similar to those recorded passaging upstream on the spillway suggesting that a broad size range could move over the structure under most flow conditions (Figures 6 and 7). However, very few smaller fish (<50 mm TL, that were present in the resting pools) were recorded moving upstream over either structure in August 2010 or 2011, nor September 2010 on the bypass. Similar patterns generally existed in length-frequency distributions between the years with smaller fish (<50 mm TL) being recorded utilising the bypass and spillway fishways mostly in September (particularly the spillway) and

October. The length-frequency distributions on the bypass fishway were generally similar between those fish moving upstream and downstream. However, on the spillway, larger fish (>50 mm TL) were mostly recorded passaging upstream versus downstream in all months sampled aside from August 2011.

As highlighted by the length-frequency distributions (Figures 6 and 7) and the density estimates (Tables 4 and 5), the Western Minnow was recorded utilising both upstream branches of Rushy Creek. Juveniles were recorded in upstream tributary habitats in September and October in 2010, and in October 2011.

The Western Pygmy Perch was captured in far greater numbers moving upstream over the bypass and the spillway in 2011 compared to 2010, particularly in October (Figure 4). Movement of the species on the bypass was generally in a downstream direction in all three months in both 2010 and 2011 with a notable large downstream movement occurring over the spillway in October 2010 and 2011, and the bypass in October 2011 (Figure 4). Negligible upstream movement of the Western Pygmy Perch on the bypass was recorded in 2010, whereas there was upstream movement on the spillway in October 2010 and upstream movements over both the bypass and spillway in October 2011.

The length-frequency analysis demonstrated that juvenile and adult Western Pygmy Perch were present in October 2010 and 2011 (Figures 8 and 9). A large upstream movement of the Western Pygmy Perch was recorded below the fishway in October 2011, which

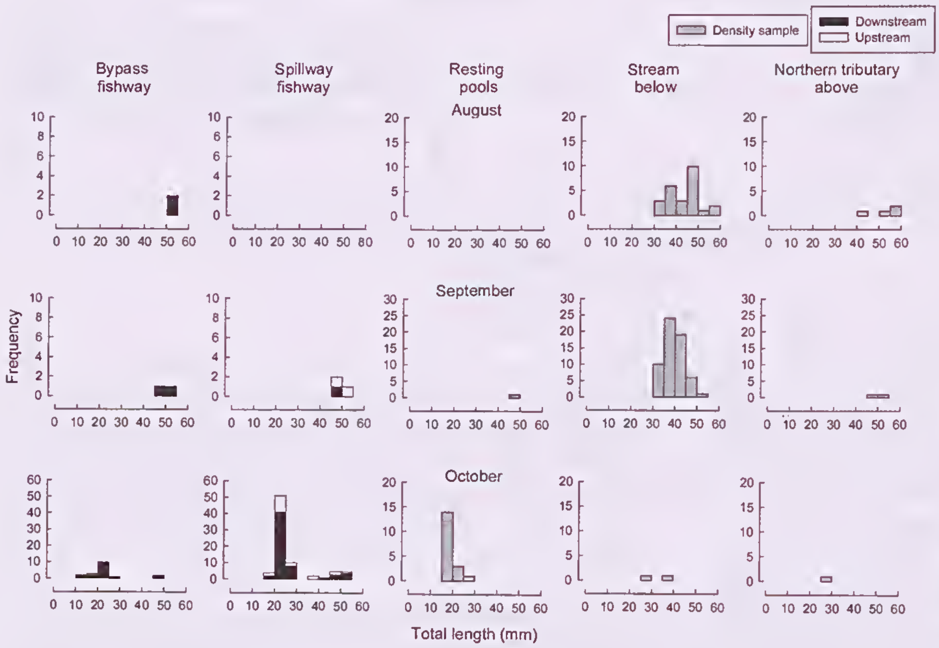

Figure 8 Length-frequency distributions of the Western Pygmy Perch in Rushy Creek at the sites and months sampled in 2010.

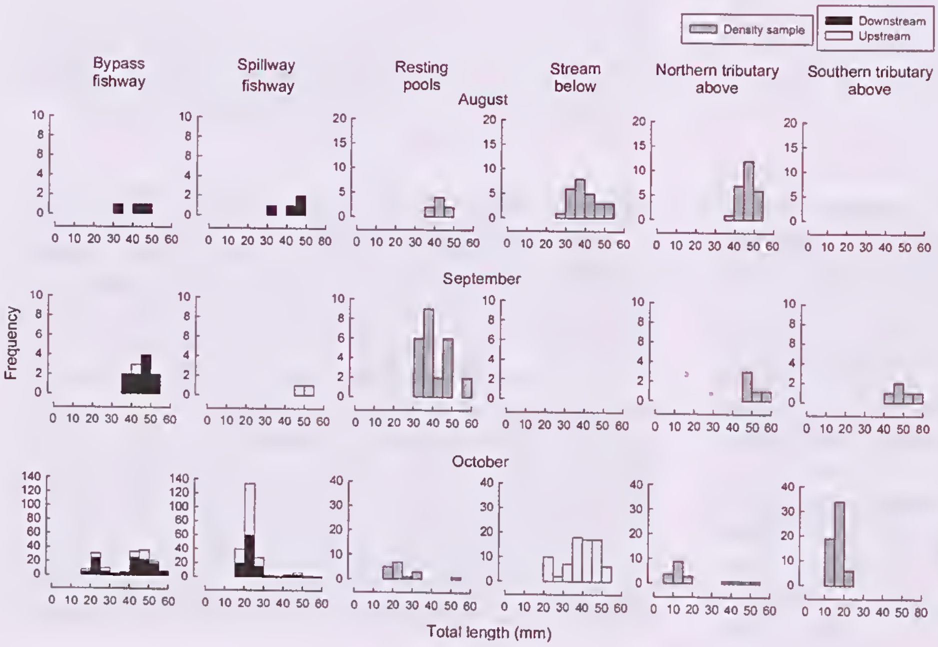

Figure 9 Length-frequency distributions of the Western Pygmy Perch in Rushy Creek at the sites and months sampled in 2011.

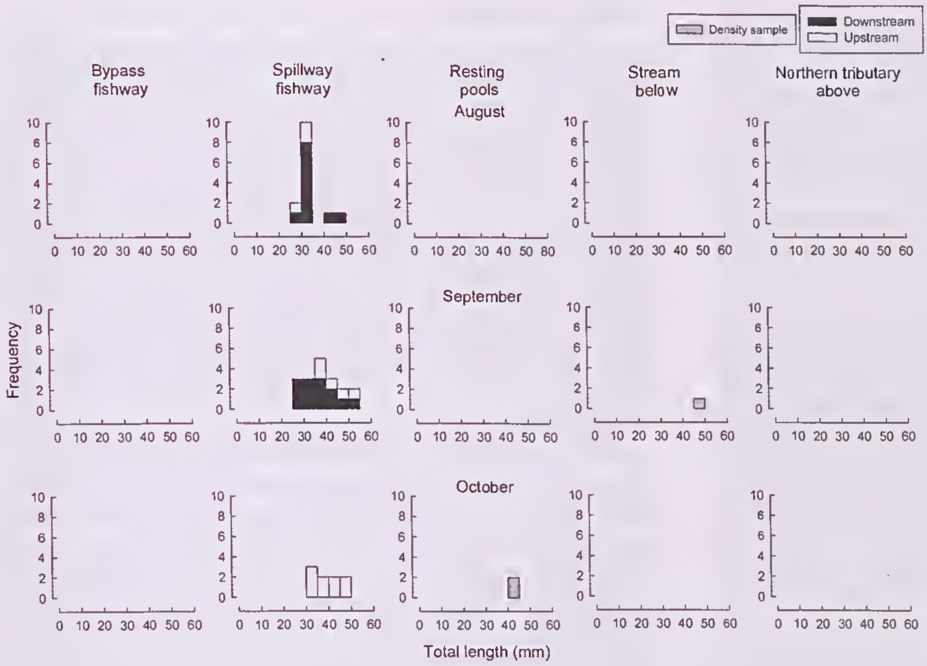

Figure 10 Length-frequency distributions of the Blue-spot Goby in Rushy Creek at the sites and months sampled in 2010.

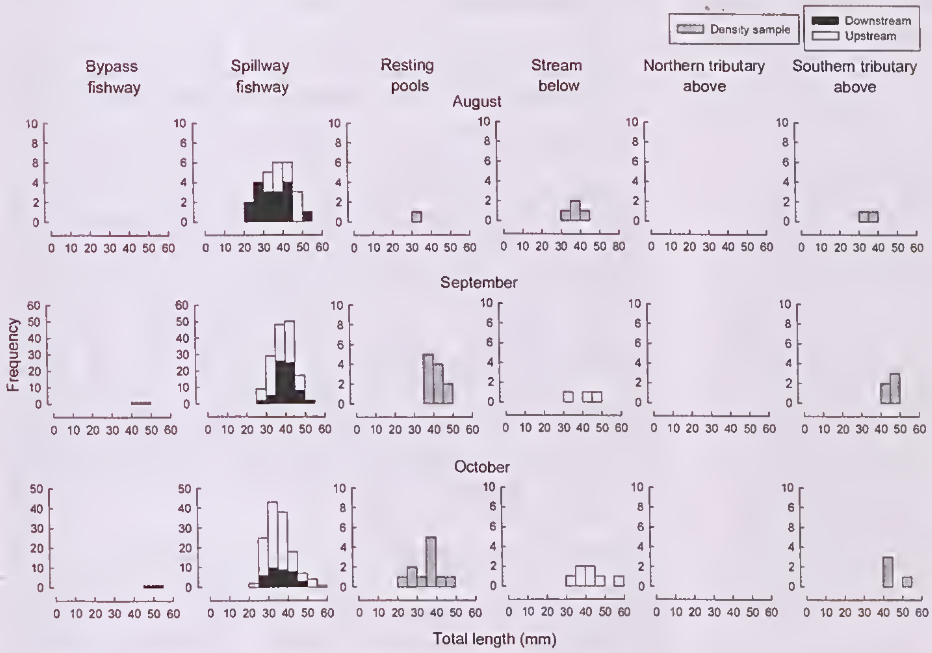

Figure 11 Length-frequency distributions of the Blue-spot Goby in Rushy Creek at the sites and months sampled in 2011.

corresponded to the large upstream movement of a wide size range over the spillway and to a lesser extent the bypass at that time (Figures 4 and 9). The modal length of juvenile Western Pygmy Perch was consistent between the 2010 and 2011 sampling periods being between 20–25 mm TL and there were no overall obvious differences in the length-frequency distributions between fish moving upstream and downstream on the fishways (Figures 8 and 9). Above the dam in the northern tributary in 2010 captures comprised of adult Western Pygmy Perch exclusively (Figure 8). However, in 2011 juvenile cohorts were present having modal lengths 10–15 and 15–20 mm TL in the northern and southern tributaries, respectively (Figures 8 and 9). Examination of the changes in density of the Western Pygmy Perch in both the northern and southern tributaries of Rushy Creek in October 2011 also showed a substantial increase between September and October (i.e. from 0.06 to 2.98 fish.m^{-2} in the northern tributary and from 0.06 to 2.97 fish.m^{-2} in the southern tributary (Table 5)). No such increase in the density of the species was recorded in the northern tributary in the 2010 sampling (Table 4). However, the upstream passage over the fishway system (mostly or exclusively over the spillway fishway) by the Western Pygmy Perch in October 2010 coincided with a considerable reduction in its density in the stream below the dam that occurred between September and October (Figure 8).

Nightfish were recorded in very low numbers moving upstream over the spillway in September 2010, and the bypass in October 2010 (Figure 4); however these captures are probably attributable to resident fish in the small section of habitat below the nets, rather than evidence of passage through the fishways. Negligible movement of the species was again recorded in those months in 2011. Additional sampling for upstream movement in Rushy Creek below the dam in 2011 also failed to detect the species; however, it was recorded in low abundance above and below the dam in both years (Tables 4 and 5).

The Freshwater Cobbler was recorded for the first time in the McLeod Creek system during the 2011 sampling (Table 5). It was recorded moving in an upstream direction below the fishways in October 2011 and was also recorded in Rushy Creek below the fishways in September and October 2011, and the lower resting pool in September 2011 (Table 5). Although captured in relatively low abundance (n = 14), the size range (i.e., 182–323 mm TL) of captured specimens represented multiple age classes and the population was therefore likely to be self-maintaining.

Blue-spot Goby was rarely recorded on the bypass (Figure 5). Captures of the species on the spillway in 2010 were dominated by downstream movements in August and September with only limited upstream movement (i.e. <5 individuals per month) being recorded in that year (Figure 5). However, similar to the Western Pygmy Perch, the species had a much greater upstream passage over the spillway in 2011 compared to 2010 (Figure 5). Upstream movement was consistently high in September and October 2011 with those months also having the greatest numbers of downstream movement over the spillway (Figure 5). The species was also recorded in relatively low numbers moving upstream in Rushy Creek below the dam in September and October 2011 (Figure 5). A relatively wide size range of the Blue-spot Goby was recorded moving upstream and downstream over the spillway, although in October 2010 and 2011 captures were dominated by upstream moving individuals (Figures 10 and 11). The Blue-spot Goby was recorded in Rushy Creek below the dam during all sampling events in both 2010 and 2011, and in the resting pools in both years (Tables 4 and 5). The species had not previously been recorded in the northern tributary above the dam but was recorded in the southern tributary in all months in 2011 (Tables 4 and 5, Figure 11).

The South-western Goby was only recorded below the dam in 2010 (September) and 2011 (September) (Table 5). Like the Western Hardyhead, the South-western Goby appears restricted in distribution to the lower reaches of Rushy Creek and McLeod Creek.

The Eastern Gambusia was found to move upstream and downstream on the spillway in very low numbers in October 2010 and 2011 (Figure 5). The Eastern Gambusia was recorded in both 2010 and 2011 on a number of occasions at a number of other sites in Rushy Creek including: below the dam, within the resting pools, and in low abundance in both the northern tributary (September and October 2010) and southern tributary (August 2011) (Tables 4 and 5). Goldfish *Carassius auratus* was also recorded below the fishways in August 2011 (Table 5).

DISCUSSION

The abundance of a number of south-western Australian freshwater fish undertaking upstream spawning migrations are positively related to amount of discharge during the peak flow periods (Beatty *et al.* 2014). The Rushy Creek fishway system was found to facilitate the upstream and downstream passage of three of the eight native fishes known to occur in the system, including the Western Minnow, Western Pygmy Perch and Blue-spot Goby. Native species that were known from the system that effectively did not passage upstream over the fishway included the Nightfish, Western Mud Minnow, Freshwater Cobbler, South-west Goby, and Western Hardyhead.

Higher rainfall and corresponding higher and more sustained stream flow occurred in 2011 *cf* 2010 (Australian Bureau of Meteorology 2014). Significantly greater numbers of fish were recorded moving upstream through the fishways in 2011 (4183 individuals) compared to 2010 (1760 individuals); which is consistent with the hydroecological relationships of Beatty *et al.* (2014). Significant differences also existed between the three most abundant species in terms of the number moving upstream and downstream and a significantly greater number of fish passed upstream through the spillway compared to the bypass.

Hydrology (principally discharge and flow rates) and life-cycles of these species explain many of those fishway usage patterns that were observed. The Western Minnow was the dominant user (in terms of abundance) of the Rushy Creek fishway system and is a species that undergoes annual potamodromous migrations (Beatty *et al.* 2014). It managed to successfully pass through both fishways in all months; including when the average flow velocity was ~97 cm.sec^{-1}. The Western Minnow spawns between early winter and mid-spring and therefore the current sampling occurred towards the latter part of its breeding period (Pen & Potter 1991a; Beatty *et al.* 2014). The length-frequency distributions of the Western Minnow in the resting pools and also those moving upstream and downstream over the fishways indicated they were negotiable by multiple age classes; including both adults and juveniles.

The Western Minnow was recorded utilising both upstream tributaries of Rushy Creek that provide spawning habitats for the species. South-western Australian freshwater fishes generally retreat downstream to permanent aquatic habitats (usually refuge pools) during the annual dry period (Beatty *et al.* 2014). As Rushy Creek is ephemeral, it is likely that at least part of the population of the Western Minnow and other species utilise the newly created reservoir as a permanent refuge habitat rather than exiting downstream through the spillway to permanent habitats further downstream. Such utilisation of large water supply dams by native freshwater fishes in the region has previously been documented (e.g. Beatty *et al.* 2003; Morgan *et al.* 2008).

The Western Pygmy Perch was also found to utilise the fishway system, albeit in lower abundances than the Western Minnow. A much stronger upstream movement of the Western Pygmy Perch occurred over both the bypass and spillway, along with an increase in downstream movement over both structures and an overall increase in abundance of the species in the upstream tributaries of Rushy Creek in 2011 relative to 2010. The Western Pygmy Perch may spawn multiple times during late winter and spring (Pen & Potter 1991b) and attain approximately 40–45 mm TL at age one. The wide size range (including juveniles) recorded moving upstream over both the bypass and spillway fishways in October 2011, and in the spillway in October 2010, suggested that the fishways may provide passage for both spawning (as indicated by adult size classes) and general population dispersal (as indicated by juvenile size classes). However, there was a relatively high abundance of larger individuals in the stream below the dam and/or resting pools in August and September in both years. This suggested a congregation of mature fish probably on an upstream spawning migration and it therefore appeared that its upstream passage over the fishways was largely precluded in August and September. It also appeared that a stronger recruitment occurred in both the southern and northern tributaries in 2011 than in the northern tributary in 2010; as evidenced by the presence of adults and juveniles in those systems in 2011 and adults in the latter system in 2010. However, a strong downstream movement of the Western Pygmy Perch occurred particularly in October with a wide size range found moving on both structures in both years highlighting that the structures were used for downstream dispersal and that recruitment had occurred in both years in the upstream habitats sampled.

Average water velocities on the spillway during October 2011 (when the largest upstream movement of Western Pygmy Perch occurred) approximated the average velocities on the bypass in that month in 2010 (when effectively no upstream passage of that species occurred). Flow velocity alone therefore does not explain the lack of upstream passage of the Western Pygmy Perch in October 2010 on the bypass. Indeed, greater and earlier onset of flows in Rushy Creek in 2011 probably facilitated an overall increase in population abundances of most species which then resulted in an overall increase in fishway passage of the Western Minnow, Blue-spot Goby and Western Pygmy Perch. During the high-flow months of August and September in both years, no upstream passage of the Western Pygmy Perch occurred at a time when a relatively high density of mature individuals congregated below the dam. It appears that hydrology on the fishways during peak flow may prevent upstream passage of the species during the majority of its spawning period. Although the bypass starts flowing earlier in the year (i.e., prior to the spillway), the relative overall greater usage of the spillway fishway by all species suggests that the bypass may be, to a degree, superfluous for facilitating fish passage. Monitoring of fish passage earlier in the year when the bypass begins to operate and flow rates are lower than those recorded in the current study, would provide greater certainty of the role of the bypass in facilitating free passage of these species.

Swimming performance of the Western Pygmy Perch, Western Minnow and Eastern Gambusia increases with size, but does not vary substantially with water temperature (Keleher 2011). Based on Keleher (2011), average velocities <65 cm.sec^{-1} over maximum distance of ~11 m should be suitable to allow the passage of Western Pygmy Perch. Based on 2010 flow data on the Rushy Creek bypass and spillway fishways, Keleher (2011) found that the greatest hypothetical distance that the Western Pygmy Perch could travel over those structures peaked in October at 1106 and 1384 cm on the bypass and spillway, respectively. Therefore, based on average velocities, the species would not have been predicted to negotiate either structure in 2010. In re-analysing this distance with the average velocities on both structures in October 2011 (see Table 2), the predicted ground distance the species could travel at its U_{sprint} would be further reduced to 896 and 1101 cm of passage on the bypass and spillway fishways (much less than their actual lengths), respectively, yet a substantial increase in passage of Western Pygmy Perch (average of ~9 fish.hr^{-1}) was recorded in October 2011. Therefore, although a very useful metric in predicting passage on structures with more uniform, laminar flow such as road culverts (Starrs *et al.* 2011), using average velocity and U_{sprint} values to predict fish passage on turbulent structures such as the cascade fishway in the current study has less utility. It is likely that the fish utilise burst swimming along with seeking low flow areas produced by the complex flow profile (see Figure 3) to successfully negotiate the fishways. It should also be noted that retrofitting of the larger steps was undertaken in May 2011 (Figure 2) both below the fishway system and particularly in the bypass that may at least partially account for the differences in the strength of passage over the fishways of the Western Pygmy Perch and other species between the years.

Although the Western Pygmy Perch can obviously travel greater distances on these fishways than would be predicted by using U_{sprint} value and average flow velocities (resulting in its successful passage in October 2010 and 2011), excessive flow rates in August and September at the time of sampling in both years (that approximated or exceeded its U_{sprint} value of 65 cm.sec^{-1}) apparently precluded its upstream passage during much of its spawning period. Furthermore, lower overall abundances of the species in 2010 and/or the presence of higher steps on the bypass and below the spillway, that were retrofitted between the sampling years, probably contributed to its lack of passage on the bypass in 2010.

The estuarine Blue-spot Goby consistently used the spillway fishway in all three sample periods in both years with almost no captures recorded in the bypass channel. That a wide size range of this species utilised the southern tributary upstream of the dam suggests that the Blue-spot Goby utilises the spillway fishway to move both upstream and downstream, and is a self-maintaining population within Rushy Creek. This species appears not to utilise the northern tributary above the dam nor the bypass channel. While swimming performance metrics need to be determined for this species, its ability to negotiate the spillway fishway may be aided by the anatomical structure of its pelvic fins; which are fused in most Gobiidae to form a suction-cup like structure that allows these species to cling onto rocks, logs or other hard substrates in high flow or turbulent conditions.

Very limited movement was observed of either the Nightfish or Western Mud Minnow on the fishway system. As the former species is known to migrate during winter and spring as part of its life-cycle (Beatty *et al.* 2014), it may be concluded that it was unable to successfully passage upstream on the fishways. However, the Nightfish was also not recorded moving upstream below the fishway during the sampling despite it coinciding with its breeding period and therefore it appeared not to be strongly migratory within Rushy Creek and it is therefore unclear as to whether it could indeed successfully passage the fishway system.

The threatened Western Mud Minnow is generally recorded in low numbers throughout its range (Morgan *et al.* 1998) and is not strongly migratory (Beatty *et al.* 2014). The downstream movement observed on the bypass channel in September 2010 indicated that it may be persisting in habitats upstream of the dam; however, no captures were recorded during population density surveys, so the size of the resident population there was probably low. The Western Hardyhead and South-western Goby were effectively not found to move upstream over either fishway and neither were they recorded moving upstream at the site below the dam (aside from the Western Hardyhead recorded once in September). All are known to occupy the main channel of the Blackwood River well inland of their typically estuarine habitats but are not commonly encountered in fresh tributaries (Beatty *et al.* 2008b, 2014). The absence of this species on the fishways is most probably due to the lack of significant migration within Rushy Creek rather than inability to negotiate them.

There are three other rock-ramp fishways that have previously been monitored in south-west Western Australia; all of these have been designed with an overall slope of 1:20 comprising 100 mm steps at 2 m intervals, inclusive of larger resting pools in-between each 1 m lift (Morgan & Beatty 2004a, b). The ratio of species observed utilising these fishway systems was generally similar to that of the current study with the Western Minnow being the dominant species. Therefore, the turbulent hydrological conditions on rock-ramp fishways are readily negotiable by the Western Minnow but much less so by sympatric freshwater fishes (Morgan & Beatty 2005; Beatty *et al.* 2007). Galaxiids, in general, are strong swimmers and can readily negotiate high velocity habitats such as riffle zones and smaller artificial barriers. Moreover, Close *et al.* (2014) demonstrated that *Galaxias truttaceus* could actually use jumping and climbing behaviour to negotiate a weir on the Goodga River, south-western Australia; despite there also being an operational vertical-slot fishway at the site (Morgan & Beatty 2006). The Western Minnow has also been observed by the primary author leaping vertically ~50 cm when attempting to pass over weirs in south-western Australia.

The number of species of introduced freshwater fishes now exceeds the number of native species in south-western Australia and there has been a sharp increase in introductions over the past decade (Beatty & Morgan 2013; Duffy *et al.* 2013). The potential passage of introduced species over barriers should be a key consideration in planning and designing fishways so as not facilitate their upstream colonisation past barriers (Beatty *et al.* 2013). The highly invasive Eastern Gambusia was recorded in both upstream and downstream fyke nets on the spillway in October 2010 and 2011. Low numbers were also captured in studies on other rock-ramp fishways in south-west Western Australia (Morgan & Beatty 2005; Beatty *et al.* 2007). This species prefers shallow, slow flowing waters and has an inferior swimming ability compared to native fishes of the region (Keleher 2011). We suspect the species was unlikely to be have undertaken upstream movement through the ~1:9 slope of the Rushy Creek fishway system. Their capture moving upstream on the fishways is most plausibly explained by the fact that the species was already present in the shallow waters on the spillway between the fyke nets and the crest, noting that this area was not cleared of fish prior to setting the nets in 2010. It is also likely that those individuals in 2011 still found their way around the blocked net as 100% blockage was not guaranteed given the small size of this species and its observed high abundances in the reservoir.

The Goldfish was also recorded in Rushy Creek for the first time having previously been recorded in very low abundance in the Blackwood River main channel (Beatty *et al.* 2008b). It was not recorded utilising the fishway system and was not recorded upstream of the reservoir. It is unlikely that the fishway system will facilitate the spread of Goldfish into upstream reaches of Rushy Creek. Therefore, whilst restricting some native species at least during higher flow periods, higher gradient fishways such as the Rushy Creek system could potentially be used where preventing introduced species passage is a priority.

The study also recorded the presence of a cestode worm in the Western Minnow population, which was probably the introduced *Ligula intestinalis* (see Morgan 2003) and caused an obvious swelling of the abdomen in infected individuals. Although present in both years, its prevalence was only quantified in 2011 when it was present in 3.3% of Western Minnows upstream of the dam and 4.3% of those downstream of the dam (including the fishways), and was most prevalent in August (9.4%) and September (2.0%). The impact of this and another introduced parasite *Lernaea cyprinacea* (Marina *et al.* 2008) on the region's freshwater fish requires ongoing research.

The study highlights the benefit of quantifying interannual variation in fishway usage. Replicating the sampling program in 2011 revealed that a wide size range of the Western Pygmy Perch could negotiate upstream over the bypass and spillway fishways in October 2011 (and spillway in October 2010) including both juveniles and adults. Sampling upstream movements and densities in Rushy Creek at the site below the dam also provided valuable information as it demonstrated that both adult and juvenile Western Pygmy Perch undertook strong upstream movements below the fishway system in October which corresponded to the species also moving over both the spillway and the bypass fishway at that time; however, it was probably unable to negotiate either fishway in August and September when congregations of adults were detected below the dam. Furthermore, the Freshwater Cobbler (the largest native south-western Australian freshwater fish) appeared unable to utilise either the bypass or spillway fishway as it is known to migrate in large numbers through riffle zones (Beatty *et* *al.* 2010). It is suggested that a substantial reduction in riffle slopes and cascades and an increase in water depth would improve fishway passage success for this species.

CONCLUSIONS

The study demonstrated that the Rushy Creek bypass and spillway structures were successful in allowing upstream passage of three of the four known migratory species in the system. The fishway system was also utilised for downstream dispersal of those species. While the bypass channel allowed upstream passage under low flow rates for a less mobile species and may allow earlier passage of resident species (i.e. early winter), greater overall utilisation of the spillway fishway was recorded for key species. The Western Minnow was shown to successfully passage upstream through the fishway system during the peak flow period of the sampling (i.e. ~97 cm.sec^{-1}).

The hydrological characteristics of the fishways along with the current limited understanding of swimming performance of the fishes help explain some but not all of the fish passage success. Other swimming performance metrics, particularly burst swimming, need to be quantified for south-western Australian species. Furthermore, the fine-scale movement patterns of fishes on fishways and indeed in unregulated rivers should be further investigated using mark-recapture. For the larger species (i.e. >~80 mm, such as most galaxiids of the region), this could involve telemetry utilising passive integrated transponders (PIT tags) and electronic monitoring stations (e.g. above and below fishways). For smaller species individually coded visible implant elastomer (VIE) tags and manual monitoring could be utilised.

Fishways have the potential to help offset the combined impacts of ongoing flow reductions and instream barriers on the migration of freshwater fishes in south-western Australia. Our results suggest rock-ramp fishways with 20 m long cascades (with maximum slopes of ~1:9) can provide varying degrees of native fish passage over relatively large on-stream dams in the region. However, as with previous studies in this region, our findings suggest more gradual riffle slopes and cascades are required to enable passage of a greater number of the migratory species (and potentially for a longer annual period). Designs should also include defined resting pools and, to enhance fishway longevity, the anchoring of ridges could be undertaken. It is also recommended that earth-movers experienced in fishway construction be employed and that designs should ensure that there are neither extended smooth sections nor any significant steps present.

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Native and non-native fishes in wetlands of the Swan Coastal Plain, Western Australia

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Fish populations in enclosed wetlands on the Swan Coastal Plain, Western Australia, were sampled to determine their species composition and distribution. Many wetlands in this area previously classed as perennial were found to not contain permanent freshwater during the sampling period between January and July 2010. Of the 113 wetlands that contained water, 76% also housed fish. Of those inhabited wetlands, few contained only native species (12%), while the many contained either both native and non-native fishes (45%) or non-native fishes only (42%). Only seven wetlands out of the 113 contained only obligate freshwater fishes native to the region. Overall, numbers of fish were dominated by the non-native species *Gambusia holbrooki* (78.6%), with the native euryhaline *Pseudogobius olorum* being next most abundant (16.2%). *Galaxias occidentalis, Leptatherina wallacei, Nannoperca vittata, Bostockia porosa* and *Galaxiella nigrostriata* were the only other native fish species caught. Wetlands with higher salinity typically contained a greater proportion of *P. olorum* and fewer *G. holbrooki*. *Nannoperca vittata* were only relatively abundant in wetlands containing dense riparian and aquatic vegetation. These trends indicated that environmental factors may convey a competitive advantage for native over non-native species, e.g. salinity for *P. olorum* and vegetation for *N. vittata*. Overall, this study highlights the paucity of lentic systems on the southern Swan Coastal Plain in which native fish populations exist without non-native competitors.

KEYWORDS: south-western Australia, freshwater fish, alien, feral

INTRODUCTION

The wetlands of the Swan Coastal Plain (SCP) in south-western Australia form a series of water bodies that are now largely isolated from each other, a situation exacerbated by the metropolitan and suburban areas by which many are now surrounded (Balla & Davis 1993). Over the past *ca* 70 years, concerns have been expressed regarding a drying trend for previously perennial water bodies. These concerns were first raised due to their agricultural value as a water source for crops and livestock (Havel 1975), but continues in response to their conservation and aesthetic value (Balla & Davis 1993). In addition to the climatically-driven drying trend (CSIRO 2009), many wetlands on the SCP have been actively cleared, drained or filled for reclamation of land, resulting in the loss of up to 80% of the original number (Bekle & Gentilli 1993; Brearley 2005). Concomitantly, groundwater abstraction and modifications to catchments have resulted in many seasonal wetlands becoming dry year round, and some perennial wetlands becoming seasonally or permanently dry (Balla & Davis 1993). This loss of permanent water prevents the survival of most fish in these lentic ecosystems. Other threatening processes for these wetlands include the introduction of non-native fauna (Morgan *et al.* 2004; Beatty & Morgan 2013), altered water quality (Davis *et al.* 1993) and urbanisation (Balla & Davis 1993; Davis & Froend 1999).

Eleven native fishes have been recorded from the freshwater lotic and lentic systems of the SCP (Morgan *et al.* 2011). Four are obligate freshwater inhabitants, *Nannoperca vittata* (Castelnau, 1873), *Bostockia porosa* Castelnau, 1873, *Tandanus bostocki* Whitley, 1944 and *Galaxias occidentalis* Ogilby, 1899 (Allen *et al.* 2002). Three others, *Nannatherina balstoni* Regan, 1906, *Galaxiella nigrostriata* (Shipway, 1953) and *Galaxiella munda* McDowall, 1978 have only been reported sporadically from the SCP but are more common in the southern parts of south-western Australia (Morgan *et al.* 1995, 1998, 2011; Smith *et al.* 2002a; Galeotti *et al.* 2010). Likewise, the diadromous species *Geotria australis* Gray, 1851 is typically found in more southern locations (Morgan *et al.* 1998). The remaining three species, *Afurcagobius suppositus* (Sauvage, 1880), *Pseudogobius olorum* (Sauvage, 1880) and *Leptatherina wallacei* (Prince, Ivantsoff & Potter, 1982), have been found in the same waterbodies (Allen *et al.* 2002) but are euryhaline species, occurring in both fresh and estuarine habitats (Morgan *et al.* 1998, 2011; Morgan & Gill 2000). All of the above species, except *P. olorum* and *G. australis*, are endemic to the Southwestern Province (Morgan *et al.* 2011). It should also be noted that as *G. australis* undertakes migrations, it predominantly inhabits lotic systems, not enclosed wetlands, and will not be considered further in this document.

Several non-native freshwater fishes have been reported from the SCP, with *Gambusia holbrooki* Girard, 1859 being by far the most widely distributed (Morgan *et al.* 2004). Other non-native species reported for this area include, *Amatitlania nigrofasciata* (Gunther, 1867), *Bidyanus bidyanus* (Mitchell, 1838), *Carassius auratus* (Linnaeus, 1758), *Cyprinus carpio* Linnaeus 1758, *Geophagus brasiliensis* (Quoy & Gaimard, 1824), *Macquaria ambigua* (Richardson, 1845), *Oncorhynchus mykiss*

(Walbaum, 1792), *Perca fluviatilis* Linnaeus, 1758, *Phalloceros harpagos* Lucinda, 2008, *Puntius conchonius* (Hamilton, 1822), *Leiopotherapon unicolor* (Günther, 1859) *Salmo trutta* Linnaeus, 1758 and *Tandanus tandanus* (Mitchell, 1838) (Beatty & Morgan 2013; Duffy *et al.* 2013).

While the distribution of freshwater fishes of south-western Australia has been relatively well documented, emphasis has been placed on those in rivers and streams (e.g. Morgan *et al.* 1998, 2004, 2006). Comparatively little work has been documented on the fish fauna of the perennial lentic water bodies in south-western Australia, particularly those of the SCP. Published reports include those by Major (2009), which documented fishes from 29 urban wetlands, and Davis *et al.* (1993), which recorded fishes caught incidentally during sampling for macroinvertebrates in 37 wetlands. Fairhurst (1993) also studied the feeding ecology of several species and single-species studies were also produced for *G. nigrostriata*, incorporating SCP wetlands (Smith 2002a, b; Galeotti *et al.* 2010). Duffy *et al.* (2013) presented the first record for Western Australia of the non-native species, *Amatitlania nigrofasciata* in a natural water body as well as providing an up-to-date catalog of non-native freshwater fish species in the region. While the information that these studies collectively provide on the fish fauna in SCP wetlands is valuable, there remain significant gaps in the body of knowledge in this area.

The aim of the current study was to address this paucity of information through a survey of the perennial wetlands of the SCP to determine the current distribution of both native and non-native fishes. As these water bodies are largely isolated from each other, it was expected that they would be relatively resilient to the spread of non-native fishes to interconnected rivers and streams. It was expected that most sites that held permanent water would contain populations of native fishes and that native fishes would be more widely distributed than non-native species. Additionally, the study aimed to explore the relationships between the relative abundance of the fish species and physical and chemical attributes of the wetlands. Information gathered during this survey will enable better prioritisation and management of water bodies, potentially including rehabilitation, non-native eradication, and feasibility assessments for restocking with native species.

METHODS

Study area and site selection

The SCP is located on the south-western coast of Western Australia. It is a narrow (30 km at its widest point) stretch of land bounded by the Indian Ocean to the west and the Darling Escarpment to the east. The region extends from Jurien Bay, approximately 600 km south to Cape Naturaliste (Cummings & Hardy 2000) and contains approximately 80% of the human population of Western Australia (Australian Bureau of Statistics 2012). The locations of the recorded perennial wetlands within the boundaries of the SCP were extracted from the Geomorphic Wetlands Swan Coastal Plain Database (Department of Environment and Conservation 2011), and overlayed on the most recent aerial photography available through various sources (Landgate, Google earth and others). The wetlands that appeared to contain permanent water were identified from those combined data sets. In many cases, individual wetlands were found to be part of small contiguous wetland complexes, each of which were subsequently considered as a single water body for sampling and analyses. Using those defined units, water bodies were discrete and physically isolated from each other. The subset of wetlands most likely to contain water were visited in the field to validate whether a permanent water body existed at that location, and when water was present, sampling for fish was conducted. Where possible, wetlands were selected from diverse locations throughout the study area to give a more representative spatial coverage of the wetlands and their fish fauna.

Sampling

Fish were sampled from 113 wetlands between January and July 2010. Climate data for the Perth metropolitan area indicated that the preceding year, 2009, was the second hottest to date (mean temperature 25.0°C, 0.6°C above the long term average) and among the 10 driest on record (annual rainfall = 608.5mm, 245.8mm below the long term average) (Bureau of Meteorology 2010).

Fish were captured using fyke nets which comprised an unbaited, 5 m single wing with 4 mm knotless mesh. Wing drop was sufficient to extend from the surface to the substrate. Up to four nets were set in some of the larger wetlands, whereas in smaller water bodies only a single net was set. They were positioned to sample both the shallow and deeper central parts of the water body. Nets were set during daylight hours, left overnight and retrieved the following day; resulting in an approximately equal soak time for each location. When nets were retrieved, fish were identified according to Allen *et al.* (2002), counted and where possible, native fish were returned to the water alive. Counts were semi-quantitative, with numbers under 200 being directly counted while numbers over 200 were estimated to the nearest 50 individuals. Fyke nets were used as a standardised sampling device due to their efficiency and as other sampling methods such as electrofishing and seine nets were inappropriate or impractical for use in many locations surveyed. The limitations of and biases introduced through using this single gear-type are acknowledged and include gear selectivity and reliance on active fish movement.

Several abiotic characteristics were recorded for each wetland including water depth (m), temperature (°C), pH, salinity (‰), dissolved oxygen (mg/L), and Secchi depth (m). The coverage of riparian vegetation of the wetland as a whole was noted, and given a score between 1 and 6 where 1 represented completely bare, and 6 represented dense fringing vegetation extending into emergent and submerged aquatic vegetation (*sensu* Keighery 1991; Major 2009). Note that vegetation was scored from a habitat complexity perspective, and as such the composition in terms of native or introduced species was not considered.

Analyses

The number of each fish species caught from each wetland was standardised to individuals/net to allow comparison across all locations. Prior to further analysis, abundances of fishes were $\log_{10}$ transformed due to the skewed nature of the abundance data as was evident on inspection of draftsmans plots of the data. Salinity was the only abiotic parameter that required (square-root) transformation. The abiotic data set was normalised prior to subsequent analyses to allow the abiotic factors measured in different units to be on the same scale and to contribute equally to the analyses.

One-way Analysis of Similarity (ANOSIM) tests were used to determine if the abiotic characteristics of the wetlands differed significantly according to whether they were inhabited by native only, non-native only, native-dominated mixed, or non-native dominated mixed assemblages. When significant differences were detected using ANOSIM, Similarity Percentages (SIMPER) was employed to determine which of the abiotic characteristics was responsible for those differences.

In order to determine if significant relationships existed between the compositions of the fish assemblages and the abiotic characteristics of the wetlands, a BioEnv test was employed. This test matched the rank similarity of the wetlands based on the abundance of the fish species present (Bray-Curtis similarity) with comparable matrices constructed for every combination of the six abiotic characteristics (Euclidian distance). The variable, or group of variables, that provided the best match to the matrix based on the fish assemblages was then determined. ANOSIM, SIMPER and BioEnv tests were all conducted using PRIMER v6 (Clarke & Gorley 2006).

RESULTS

Sampling locations and dry wetlands

The Geomorphic Wetlands Swan Coastal Plain Database indicated that more than 4,000 perennial wetlands exist on the SCP. Comparison of aerial photography and the wetlands database indicated only *ca* 2,000 discrete water bodies were present, with many wetland complexes containing several that may be seasonally contiguous. Only 806 of those discrete water bodies appeared to contain water with the majority of these occurring on the southern half of the SCP (Figure 1). Of those 806 wetlands, 366 were visited in the field, however, many that appeared to contain water from the aerial photographs were actually dry during the sampling period (89 wetlands; 24%; Figure 1) or were inaccessible (164 wetlands; 45%). Both the elevated temperature and decreased rainfall during the preceding year are likely to have contributed to the very large number of dry wetlands observed.

Consequently, of the *ca* 2,000 discrete mapped perennial wetlands, 113 were sampled for fish. The mean salinity in these wetlands was low (2.3 ‰, SD=5.4 ‰), but ranged between 0 and 33 ‰. The mean depth was only 1.2 m (SD=0.8 m) but varied considerably with several very shallow (0.2 m) and deep (4 m) wetlands sampled.

Fish fauna

Fish were caught in 76% (n=86) of the 113 wetlands sampled. Non-native fishes were present in a greater proportion of inhabited wetlands (86%, n=75) than native fishes (57%, n=50). Likewise, there were more wetlands that contained exclusively non-native fishes (42%, n=36) than exclusively native fishes (12%, n=11) (Table 1; Figure 2a). Mixed assemblages containing both native and non-native species were found in 45% of inhabited wetlands (n=39). When they co-occurred, native fish outnumbered non-native fish in 56% of wetlands, the non-natives were more abundant in 26%, while the remaining 18% of wetlands contained native and non-native fish in approximately equal numbers. The distribution data for all fish species in this study are maintained by the Western Australian Department of Fisheries in the

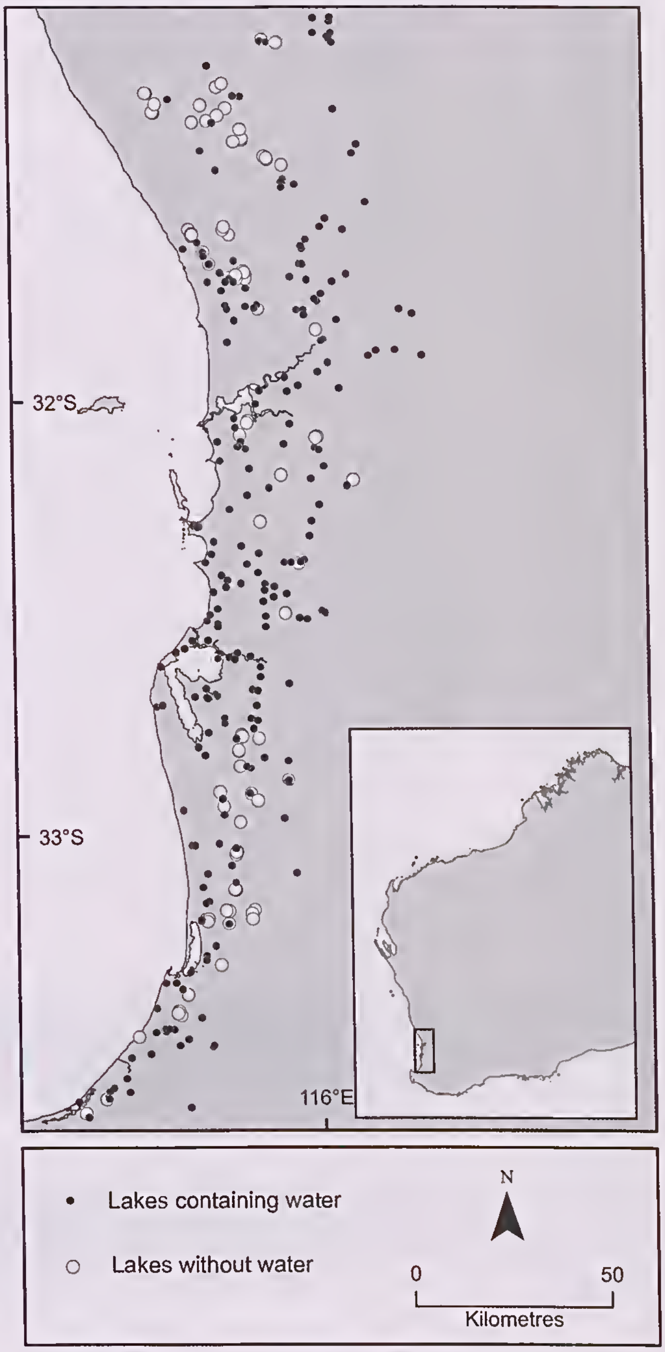

Figure 1 Map of the southern Swan Coastal Plain showing the location of those water bodies which were visited in the field and either confirmed to hold water or found to be dry. Inset showing the location of the study in relation to Western Australia.

Table 1 The details for each wetland sampled including the Geomorphic Wetlands database reference number, latitude and longitude of sampling area and the presence or absence of each of the fish species. N.B. Presence is denoted with an "X". Species codes are: *Po* = *Pseudogobius olorum*, *Go* = *Galaxias occidentalis*, *Lw* = *Leptatherina wallacei*, *Nv* = *Nannoperca vittata*, *Bp* = *Bostockia porosa*, *Gn* = *Galaxiella nigrostriata*, *Gh* = *Gambusia holbrooki*, *Td* = *Tandanus tandanus*, *Lu* = *Leiopotherapon unicolor*, *Ca* = *Carassius auratus*, *Pc* = *Puntius conchonius*, *Xh* = *Xiphophorus hellerii*, *Gb* = *Geophagus brasiliensis*.

Geomorphic wetlands identification number	Latitude	Longitude	Native fishes						Introduced fishes						
			Po	*Go*	*Lw*	*Nv*	*Bp*	*Gn*	*Gh*	*Td*	*Lu*	*Ca*	*Pc*	*Xh*	*Gb*
41BN 1269	-33.60127	115.49864	X						X						
41BN 1274	-33.61232	115.42963	X												
41BN 685	-33.64800	115.45157		X											
41BQ 3700	-33.62572	115.69027													
42BO 3159	-33.55868	116.54061	X	X					X						
42BO 734	-33.51222	115.55304	X						X						
43BP 1041	-33.45226	115.61112		X					X			X			
43BP 3157	-33.45146	115.63401	X						X						
43BP 3684	-33.44447	115.63164							X			X			
43BP 3977	-33.44432	115.62983							X						
43BQ 2375	-33.41926	115.71635							X						
43BQ 2382	-33.48620	115.74297													
44BP 3991	-33.39767	115.61342							X						
44BQ 2376	-33.35276	115.67501	X						X			X			
44BQ 2901	-33.35518	115.67534	X						X			X			
45BR 704	-33.25366	115.75207	X	X					X						
47BQ 725	-33.08750	115.73471							X						
48BR 4215	-33.01770	115.76375													
49BS 1933	-32.92063	115.85497													
50BS 3598	-32.84357	115.83784							X						
50BT 1684	-32.87859	115.92829													
51BQ 3870	-32.81488	115.73280							X			X			
51BR 2517	-32.77632	115.80560		X			X								
51BS 2254	-32.75301	115.84889		X											
51BS 493	-32.75280	115.84637							X						
52BR 202	-32.91459	115.77197													
52BR 667	-32.67739	115.76331													
52BS 2412	-32.73009	115.84131							X						
52BS 580	-32.70030	115.85358							X						
53BP 2039	-32.60923	115.63214													
53BP 2497	-32.61155	115.63304													
53BQ 294	-32.66070	115.73763													
53BR 3075	-32.59005	115.79304	X						X						
53BS 2564	-32.61234	115.86475	X	X											
53BS 666	-32.58763	115.84092													
54BQ 1175	-32.50361	115.74268							X						
54BQ 2661	-32.57764	115.66867							X						
54BQ 2720	-32.50588	115.74193							X						
54BQ 3216	-32.55074	115.70766	X						X						

Geomorphic wetlands identification number	Latitude	Longitude	Native fishes						Introduced fishes						
			Po	*Go*	*Lw*	*Nv*	*Bp*	*Gn*	*Gh*	*Td*	*Lu*	*Ca*	*Pc*	*Xh*	*Gb*
54BQ 3358	-32.55000	115.74341							X						
54BQ 475	-32.56871	115.68805	X												
54BR 1192	-32.51239	115.76736													
54BR 2731	-32.57835	115.81307	X												
54BR 3583	-32.51766	115.76680													
54BR 594	-32.57922	115.81137	X												
55BQ 4132	-32.49172	115.74962							X						
55BR 1174	-32.43834	115.75815							X				X		
55BR 234	-32.47692	115.76752				X			X						
55BR 3816	-32.47646	115.76752				X			X						
55BS 3113	-32.41930	115.87774		X					X						
55BT 4165	-32.49785	115.95612							X						
56BQ 3854	-32.37090	115.73952													
56BR 3047	-32.35155	115.75377							X			X			
56BS 1741	-32.39411	115.86131							X						
56BS 2562	-32.37371	115.83749	X	X					X						
56BT 1364	-32.36514	115.96985	X	X		X									
56BT 1975	-32.37282	115.95471													
56BT 258	-32.37011	115.92331													
57BQ 3299	-32.28821	115.72715	X						X						
57BR 210	-32.33315	115.82369							X						
57BR 2791	-32.32152	115.76017							X			X			
57BT 120	-32.31004	115.98153													
57BT 2404	-32.27560	115.98720							X						
58BR 897	-32.24918	115.79916													
58BT 2487	-32.17700	115.98745							X			X			
58BU 1917	-32.23802	116.00669		X								X			
59BR 2800	-32.13765	115.77780	X						X						
59BR 3490	-32.09271	115.77153							X						
59BS 2770	-32.15544	115.84384													
59BS 673	-32.10968	115.83593							X					X	
59BT 213	-32.10698	115.99697	X	X		X			X						
59BT 514	-32.09844	115.92530	X			X			X		X				
59BU 1455	-32.11205	116.00608													
60BR 1652	-32.03898	115.81144							X	X					
60BR 4093	-32.05991	115.81344							X				X		
60BS 4073	-32.00628	115.86241							X						
60BT 2573	-32.05207	115.93929	X						X						
61BS 314	-31.97401	115.87018							X						
61BT 1395	-31.94445	115.92949	X						X						
61BT 3562	-31.97662	115.93341							X						
61BU 2118	-31.93131	116.00663		X					X						

Table 1 (cont.)

Geomorphic wetlands identification number	Latitude	Longitude	Native fishes						Introduced fishes						
			Po	*Go*	*Lw*	*Nv*	*Bp*	*Gn*	*Gh*	*Td*	*Lu*	*Ca*	*Pc*	*Xh*	*Gb*
62BU 1930	-31.91009	116.03049							X						
62BU 2244	-31.85707	116.01985	X	X					X						
62BV 1401	-31.88168	116.14259							X						
63BR 201	-31.77872	115.79568	X						X						
63BR 2292	-31.78688	115.79922	X						X						
63BR 4092	-31.81317	115.81540	X						X						
63BS 2658	-31.78506	115.86143							X						
63BS 370	-31.77775	115.86774													
63BT 1508	-31.78958	115.97501					X		X						
63BT 1964	-31.78941	115.95967							X						
63BT 3729	-31.79951	115.97555		X		X	X								
63BU 3197	-31.75221	116.01691		X					X						
63BU 3523	-31.76816	116.00563	X						X						X
63BU 864	-31.76339	116.00152													
63BW 129	-31.78697	116.19564		X											
64BR 1319	-31.74369	115.78527	X						X						
64BR 4010	-31.71642	115.80421							X						
64BR 899	-31.72525	115.75573							X						
64BT 306	-31.71931	115.98397				X									
65BQ 3745	-31.63388	115.73196							X						
66BV 1605	-31.53905	116.12167	X	X			X		X						
67BS 467	-31.42507	115.88992	X	X	X				X						
67BT 2202	-31.44533	115.93795				X	X								
67BT 3609	-31.49427	115.93190													
67BT 977	-31.49903	115.95793		X			X	X	X						
67BV 1582	-31.42744	116.09189	X	X	X	X	X		X						
68BV 1854	-31.40727	116.10285	X	X	X	X	X		X						
70BR 3850	-31.86360	115.79817		X	X							X			
70BS 3077	-31.16757	115.88458													
97BM 57	-28.94392	115.38383													
98BM 8	-28.91187	115.41218													
98BN 2061	-28.89173	115.43041													

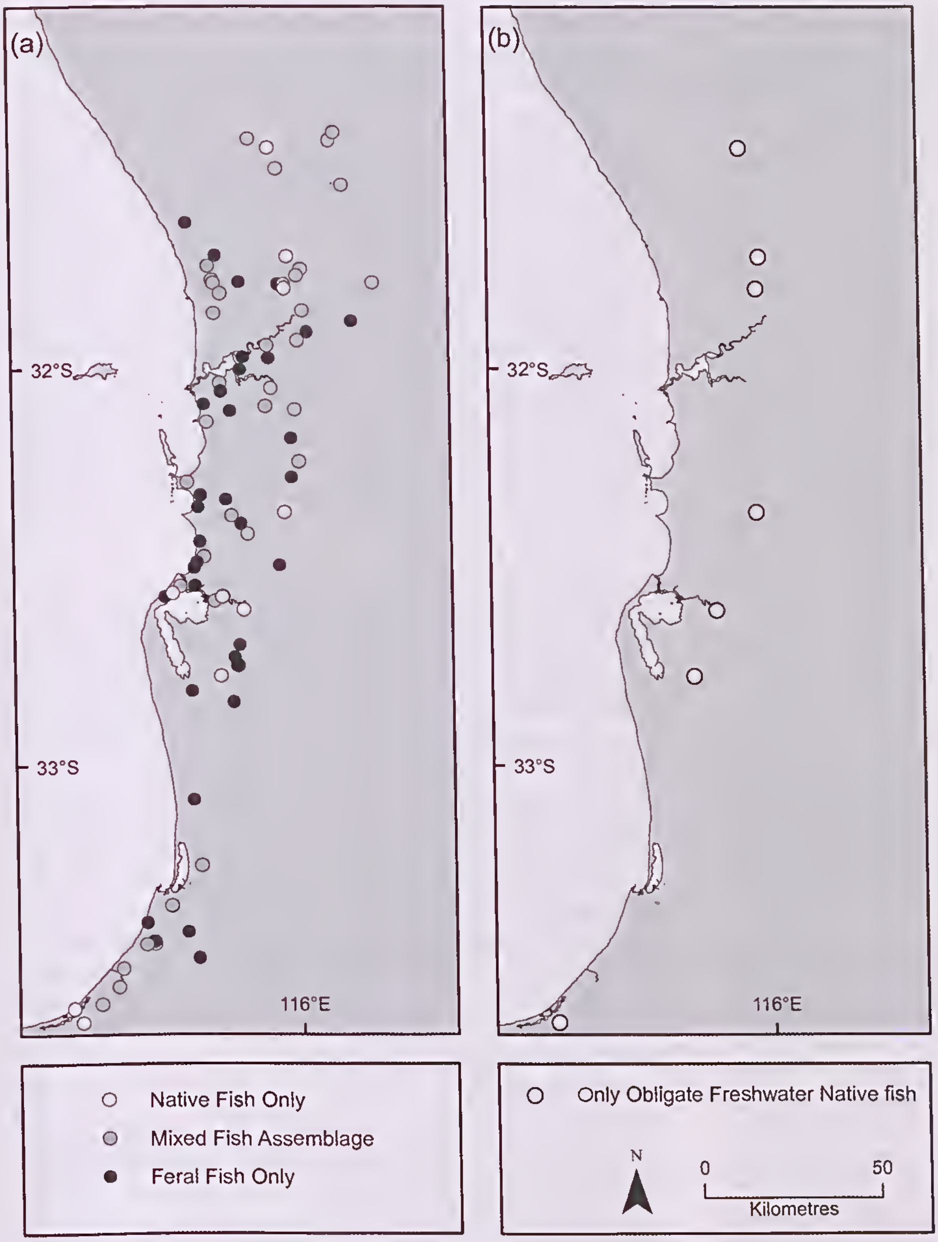

Figure 2 Map of the southern Swan Coastal Plain showing the location of those water bodies which (a) were sampled and contained fish, coded for the composition of the fish assemblages (native only, mixed or non-native only), and (b) contained only native, obligate freshwater species.

publicly available online Freshwater Fish Distribution Database (Department of Fisheries 2012).

The total number of fish caught during this study was *ca* 62,200 individuals and overall, non-native fish outnumbered native fish at a ratio of almost 4:1 (Table 2). The two most abundant species were *G. holbrooki* and *P. olorum*, which collectively accounted for 94.8% of the total number of individuals caught (78.6% and 16.2%, respectively). The remaining 5.2% of the fish caught included the native species *G. occidentalis* (2.2%) and *L. wallacei* (1.8%) as well as several other native and non-native species, each of which contributed <1% (Table 2). Four native species, whose reported distribution included the study area, were absent from samples in the current study i.e. *T. bostocki, N. balstoni, G. munda* and *A. suppositus*.

A total of seven non-native species were detected during the current survey (Table 2), including one species not previously recorded from the SCP i.e. *Xiphophorus hellerii* Heckel, 1848.

Relationships between fish assemblages and abiotic characteristics

ANOSIM determined that no significant differences existed in the abiotic characteristics of the wetlands among those that contained native, non-native or mixed assemblages. However, when only those wetlands that contained mixed assemblages were analysed separately, significant differences in the abiotic characteristics were detected between those that were dominated by natives compared to those dominated by non-native species, however, the differences were small (R=0.151, P=0.001). SIMPER determined that those differences were primarily due to salinity, which was greater in the wetlands dominated by native fishes and lower in the wetlands dominated by non-native fishes. Since the two most common species were *P. olorum* (native) and *G. holbrooki* (non-native), it can be inferred that these two species are largely responsible for the native vs non-native trends identified by the above analysis.

BioEnv determined that there was a significant relationship between the environmental characteristics of

Table 2 The total number of individuals caught (N), the percentage contribution to the total number of individuals (%) and the number of water bodies in which they were encountered (Freq) for each of the six native and seven non-native fishes found during the survey of the freshwater wetlands of the southern Swan Coastal Plain.

Species	Common name	N	%	Freq
Pseudogobius olorum	Swan River Goby	10,052	16.2	32
Galaxias occidentalis	Western Minnow	1,365	2.2	23
Leptatherina wallacei	Western Hardyhead	1,111	1.8	4
Nannoperca vittata	Western Pygmy Perch	334	<1	10
Bostockia porosa	Nightfish	57	<1	8
Galaxiella nigrostriata	Black-Stripe Minnow	1	<1	1
Gambusia holbrooki	Eastern Gambusia	48,890	78.6	71
Tandanus tandanus	Freshwater Catfish	175	<1	1
Leiopotherapon unicolor	Spangled Perch	117	<1	1
Carassius auratus	Goldfish	62	<1	10
Puntius conchonius	Rosy Barb	58	<1	2
Xiphophorus hellerii	Swordtail	1	<1	1
Geophagus brasiliensis	Pearl Cichlid	1	<1	1

the wetlands and the composition of fish assemblages, but that the correlation was low. The greatest, significant correlation for the rank similarity of wetlands between abiotic characteristics and the fish datasets was for a combination of salinity, water depth and vegetation score (ρ=0.279; P=0.01).

When the abundances of the *P. olorum* and *G. holbrooki* were examined in relation to wetland salinities in more detail it was determined that six of the seven highest abundances of *P. olorum* occurred in wetlands with salinity greater than 1‰. Conversely, 11 of the 12 highest abundances of *G. holbrooki* occurred below this same salinity threshold. Catches of *G. holbrooki* averaged only 26 individuals.net^{-1} in wetlands with a salinity greater than 1‰, whereas below that salinity, the average catch was 270 individuals.net^{-1}, and the maximum recorded was 5000 individuals.net^{-1}.

Only 10 of the surveyed wetlands contained *N. vittata* of which all had scores for vegetation greater than 3. Furthermore, the largest numbers of this fish were found in wetlands with vegetation scores of 5 or 6.

DISCUSSION

This study highlights that many of the wetland habitats on the SCP identified as perennial no longer hold permanent water, and that in those remaining wetlands non-native fish outnumber native fish considerably. It follows then, that the native fish populations in the wetlands of the SCP are under considerable pressure from both habitat loss and interactions with non-native fish species. The number of perennial wetlands that are capable of supporting fish is much smaller than historically recorded and native fish in this region are far less numerous and less widely distributed than non-native species. Also, a number of species previously reported from the region were not found during this study. The wide distribution of non-native fish in the wetlands of the SCP indicates that the non-contiguous nature of these water bodies has not presented a significant barrier to the spread of non-native fishes.

Although the primary focus of the project was to survey the fish faunas of the perennial wetlands of the SCP, it included by necessity, determination of which water bodies that were previously recorded as perennial continued to be so. The results from this study indicate that many of the perennial wetlands recorded by the Geomorphic Wetlands Swan Coastal Plain dataset did not hold permanent water during the survey period. This obviously has significant ramifications for the fishes of the region. As previously noted, the wetlands of the SCP are subject to drying as a result of several pressures including a general climatic drying trend, groundwater abstraction and active drainage (Davis & Froend 1999). On top of these factors, the year preceding the survey was both considerably hotter and drier than the annual averages for the region.

It is acknowledged that additional habitats other than enclosed wetlands exist for freshwater fish on the SCP, including artificial impoundments, rivers and streams (e.g. Morgan *et al.* 1998, 2004, 2006; Morgan & Beatty 2008). While these water bodies have been reported to contain populations of native fishes, more surveys are required to update contemporary distributions. While these other environments may act as refuges for remnant populations across the study area, these water bodies are also susceptible to the drying trend affecting the wetlands of the region. Likewise, while substantial populations of native fishes are located in the southern regions of south-western Australia, particularly in wilderness areas, the loss and degradation of habitat in the urbanised Perth metropolitan area and more generally the SCP, represents a significant loss for native fish biodiversity through range contraction and fragmentation, with a likely decrease of genetic diversity.

Non-native fishes are more widely spread in the wetlands of the SCP and outnumber native fishes overall by four to one (relative survey abundance). *Puntius conchonius* has previously been reported on the SCP (Duffy *et al.* 2013) as well as further south (Beatty *et al.* 2006) and was found at two locations during this survey. *Xiphophorus hellerii* has been found to the north of the SCP (Morgan & Gill 2001) and was only found once on the SCP during this survey. *Tandanus tandanus* was recorded in water bodies of Western Australia by Duffy *et al.* (2013) and was present in only one water body.

Despite the prevalence of non-native fishes, the patterns of abundance of both native and non-native species indicate that some native fishes have a degree of resilience to the presence of non-native fish. Analysis of the assemblage composition of the fish faunas indicates that native fish populations have similar, or greater, relative abundances when they co-occur with non-native species as they do in native-only wetlands. This is not the case for non-native species, which are in much lower abundances when they co-occur with native species than in non-native-only wetlands. One possible cause for these patterns of abundance, which is somewhat supported by analysis of environmental characteristics, is that the salinity of the wetlands, coupled with the differing responses to salinity of the two most abundant species (*G. holbrooki* and *P. olorum*) creates a threshold that mediates their competitive success, i.e. in many wetlands with lower salinity, *G. holbrooki* are able to proliferate to the exclusion of native species. However in wetlands with slightly elevated salinity *P. olorum* is able to maintain a competitive advantage over *G. holbrooki*. The concept that salinity may mediate non-native vs native interactions is supported by the results of other studies. Alcaraz *et al.* (2008) examined changes in the interactions between *G. holbrooki* and the Mediterranean Killifish, *Aphanius fasciatus* (Valenciennes, 1821) at different salinities, demonstrating that at higher salinities *G. holbrooki* became less efficient predators and were less antagonistic toward co-habiting fish, while the other species was not similarly affected. It is not suggested that *G. holbrooki* is intolerant of higher salinities, as records of survival in saline water are available (Pyke 2005), instead that the competitive advantage that allows this introduced species to proliferate is somewhat diminished.

Further evidence that native species can effectively compete with non-native species is that a population of *N. vittata* in Mason's Lake on the SCP was present, and that individuals were reproducing, and apparently in good physical condition despite being outnumbered by *G. holbrooki* at a ratio of 30:1 (Major 2009). Just prior to the sampling for that study the lake had been intensively trapped and *G. holbrooki* removed to reduce their relative abundance from 156:1 to 30:1 (Unpublished data, Department of Fisheries). It has been postulated that the reason for this and similar instances of successful native/non-native cohabitation is the presence of dense riparian vegetation providing increased habitat complexity (Hambleton *et al.* 1996; Gill *et al.* 1999; Morgan *et al.* 2004; King & Warburton 2007; Major 2009). Our results support this assertion, since all of the wetlands in which *N. vittata* occurred in a mixed assemblage with non-native fish had moderate to high scores for vegetation cover. Furthermore, the largest populations of this species occurred in wetlands with high vegetation scores, and wetlands with low vegetation scores never contained this species. Given the high likelihood of native and non-native fishes co-occurring, the importance of maintaining or augmenting intact riparian and aquatic vegetation for any conservation and remediation actions should not be underestimated.

Four species previously reported from the SCP (Morgan *et al.* 2011) were not collected during the present survey of perennial wetlands, *i.e. T. bostocki, A. suppositus, N. balstoni* and *G. munda*. The first two species, *T. bostocki* and *A. suppositus* that were absent from samples are typically, but not exclusively, associated with lotic rather than lentic systems, with the latter species additionally occurring in estuaries (Neira *et al.* 1998; Morgan & Beatty 2008, Morgan *et al.* 2011). It is not surprising then that these species were not found, since those former environments were not the targets of this study.

Nannatherina balstoni and *G. munda* have only been recorded sporadically on the SCP, with records indicating their current core distribution is further south (Morgan *et al.* 2011). The only record of *G. munda* on the SCP is a relict population in the Ellen Brook and Lennard Brook region, and a recent report states that this population is still present, despite being well outside this species' common range, isolated, and in the same area as a considerable non-native fish incursion (Beatty *et al.* 2010). Ongoing surveys are required to determine if any other relict populations exist or if this species is otherwise absent north of Perth. Similarly, *N. balstoni* was most recently recorded from isolated populations on the SCP near the Moore River, north of Perth (Morgan *et al.* 1998), but has not been formally documented in this area since that time (Department of the Environment, World Heritage and the Arts, 2008). It is likely that this species' range has now contracted to the south.

Only a single individual of *G. nigrostriata* was encountered during this study, however this is probably a reflection of its typical habitat, ephemeral wetlands, not being the target of this study as well as its mainly southern distribution. The single location at which it was found during this study (Chandala Nature Reserve) is the same site as reported by McLure & Horwitz (2009). The other two SCP remnant populations documented by Galeotti *et al.* (2010) were not re-surveyed as they were dry at the time they were visited. This suggests that to accurately capture the distribution of *G. nigrostriata*, future sampling designs should accommodate ephemeral wetlands when they contain water. Regardless of whether *G. nigrostriata* only temporarily inhabits ephemeral wetlands and populations retreat to refuge wetlands containing permanent water during the dry months, or is able to aestivate and remain in the ephemeral wetlands, it is critical for the continued survival of this species to find and protect the wetlands in which it resides. This is equally applicable to the SCP locations as it is throughout its more southern range.

The dual pressures of habitat loss through wetland drying, and the incursion of non-native fishes appear to have drastically reduced the number of wetlands that are currently inhabited by native freshwater fishes on the southern SCP. Less than 10% of the water bodies surveyed contained only native fish, with an even smaller proportion containing only obligate freshwater species endemic to the region such as *N. vittata, G. occidentalis, G. nigrostriata* and *B. porosa* (seven wetlands, Figure 2b). These few wetlands should be highlighted as priorities for habitat conservation and receive attention for further management actions. Further study is recommended to adequately inform ongoing management. In particular, a greater spatial coverage is recommended, with the survey of fish in additional inland and northern wetlands of the Southwestern Province, and the inclusion of ephemeral water bodies to more accurately gauge the distribution of *G. nigrostriata*. Additionally, a study of the genetic stock structure of the native fishes in these wetlands will greatly inform potential management strategies such as restocking and supplementation programs as part of broader conservation efforts.

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Ecological response of an estuarine atherinid to secondary salinisation in south-western Australia

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Secondary salinisation of rivers is a major threat to aquatic ecosystems, particularly in the south-west of Western Australia. Salinisation has changed the structure of freshwater fish assemblages in the south-west, with many estuarine species now being found well inland and outside of their historic range. The current study aimed to determine whether plasticity in life-history traits, in addition to physiological tolerance, may facilitate competitive advantage of estuarine invaders in secondarily salinised systems. *Leptatherina wallacei* is a teleost endemic to the region and was historically found in the upper reaches of estuaries and several coastal lakes. Several life-history, morphological and ecological traits of *L. wallacei*, in habitats of differing salinities in the Blackwood River were determined. Our study reveals that, complementing its broad physiological tolerance to salinity, the species has flexible life-history traits, such as a protracted spawning period, early maturation, fast growth and a broad diet. Its spawning period and growth rate also differed among populations in different sections of the river, with those in the more salinised upper catchment spawning at a similar time to estuarine fish, whereas in the less salinised lower catchment, spawning was delayed for a season, reproductive activity was reduced and growth was faster. The prevalence of macroparasites was significantly greater in fish populations in the lower catchment than in the upper catchment, and this may have contributed to reduced reproductive activity. We suggest that phenotypic plasticity in life-history traits, along with broad physiological tolerance to elevated salinity and an escape from parasitic infection, has facilitated a competitive advantage to the species that has enabled it to become a dominant fish in secondarily salinised habitats.

KEYWORDS: salinity, Blackwood River, *Leptatherina wallacei*, life-history, diet, parasitism

INTRODUCTION

Secondary salinisation of rivers is a major global threat to aquatic ecosystems (Cañedo-Argüelles *et al.* 2013). It has ecological impacts on multiple scales including the individual, species and community level. Fish assemblages, in particular, are often dramatically affected by the salinisation of rivers (Higgins & Wilde 2005; Hoagstrom 2009). Differences in fish distributions in relation to salinity reflect differences in historical distribution patterns and in the ability of species to respond at the level of the individual (through phenotypic plasticity) or the population (through adaptation) to secondary salinisation. Salinisation imposes stresses on freshwater organisms both directly, for example on physiological functioning, and indirectly, such as through food availability or competitive interactions (Nielsen *et al.* 2003a).

Aquatic ecosystems in Western Australia have been severely impacted by secondary salinisation. From a fish perspective, most of the impacted areas fall within the Southwestern Province (Morgan *et al.* 2003; Beatty *et al.* 2011), although some rivers within the Pilbara Province have also been affected (Morgan & Gill 2004; Unmack 2013). Secondary salinisation within the Southwestern Province is a consequence of wide scale clearing of native vegetation during the last century and reduced rainfall. As a result, only ~44% of flow in the largest 30 rivers in the region is now fresh (Mayer *et al.* 2005). While the structural changes in fish communities in the Province are now well understood (Morgan *et al.* 2003; Beatty *et al.* 2011), little is known of how secondary salinisation has driven shifts in life-history, morphology and ecology of fishes in this region or indeed elsewhere.

Within the Southwestern Province, secondary salinisation has led to a number of species that are typically found in estuaries now being found well inland and outside of their historic range (Morgan *et al.* 1998, 2003; Beatty *et al.* 2011). One of these species is the western hardyhead (*Leptatherina wallacei*) (Atherinidae), which is endemic to the region and is widely distributed from the Hill River in the north to the east of Esperance (Figure 1), where it is often abundant in rivers, some saline lakes, a few freshwater lakes and most estuaries (Morgan *et al.* 1998; Potter & Hyndes 1999; Morgan & Gill 2004). Within the Blackwood River, the largest river by discharge in the region, *L. wallacei* is the second most abundant fish species in the estuary (Valesini *et al.* 1997) and also contributes to almost 25% of all fish abundance upstream of the estuary; presumably a consequence of secondary salinisation within this catchment, given that records of the species in the riverine sections of the catchment have been relatively recent (Morgan *et al.* 2003). Therefore, *L. wallacei* represents an ideal model

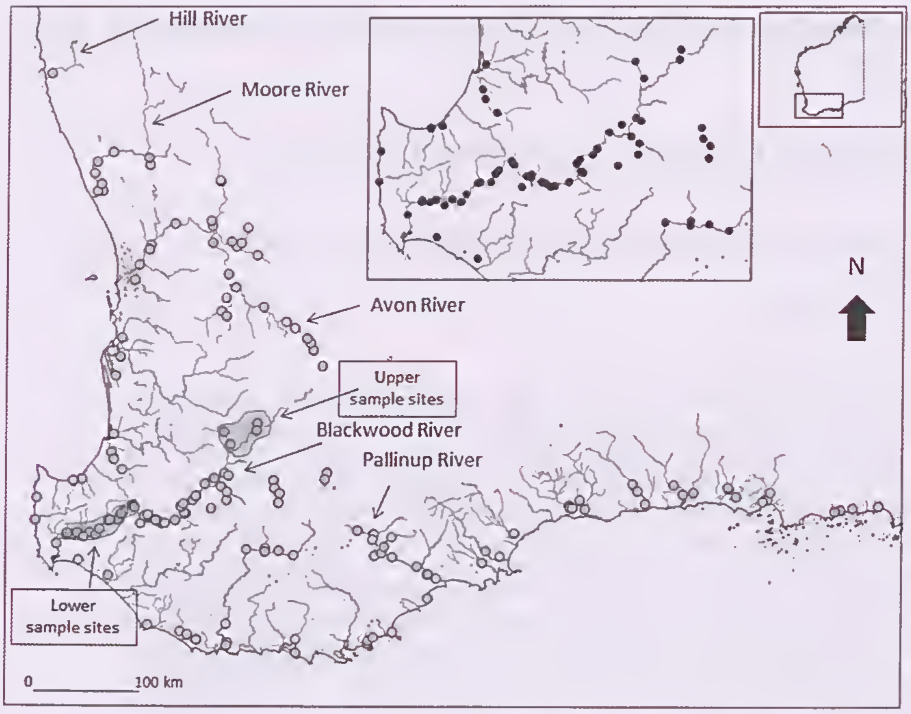

Figure 1 Distribution of *Leptatherina wallacei*, including sample site locations in the upper and lower catchment of the Blackwood River (distributional data from Morgan *et al.* 1998, 2003, 2006).

species upon which to conduct a field-based investigation of how flexibility in life-history, morphology, and ecological traits may help facilitate the exploitation of secondarily salinised systems.

Although the diet, reproductive period and longevity of *L. wallacei* have been elucidated within an estuarine environment (the Swan River Estuary; see Prince *et al.* 1982; Prince & Potter 1983), there have been no ecological studies within non-estuarine environments for this species. The aim of the current study was to quantify variability in the life-history, morphology and ecology of *L. wallacei* in habitats of varying salinity in the Blackwood River. We hypothesised that there would be considerable differences in traits between these populations, that may help explain the successful inland colonisation by *L. wallacei* of secondarily salinised systems.

MATERIALS AND METHODS

Sampling protocol

The catchment of the Blackwood River covers an area of more than 21,900 km^2 in the Southwestern Province. Increasing dryland salinity in the catchment has led to salinisation of the Blackwood River. Water salinity varies from >30 ppt in the upper catchment to approximately 1.5–4 ppt in the lower reaches of the main channel, which receives low salinity groundwater, and less than 0.5 ppt in forested tributaries which feed into the lower main channel (Morgan *et al.* 2003; Mayer *et al.* 2005; Beatty *et al.* 2011).

Four sites were selected in each of the highly salinised main channel of the upper catchment and the less salinised main channel of the lower catchment of the Blackwood River, and three sites were selected in freshwater tributaries in the lower catchment to assess the ecology of *L. wallacei* (Figure 1). Sites were sampled at approximately monthly intervals over a 12 month period in 2006. As the target species was not collected from the tributary sites, for a comparison of the biology of *L. wallacei*, sites were grouped into upper catchment or lower catchment (main channel). For some comparisons, sampling dates were grouped into wet season (June to October) or dry season (November to April).

Juvenile and adult fishes were captured at each locality using seine nets (10 or 15 m long, fishing to a depth of 2 m) or fyke nets (11.2 m wide with two 5 m wings and a 1.2 m wide mouth fishing to a depth of 0.8 m, and a 5 m pocket with two internal funnels); all nets being of 2 or 3 mm woven mesh. Collected fishes were identified to species in the field using Allen *et al.* (2002), counted and all native non-target species returned immediately to the water. Larval, juvenile or adult fish were euthanised in an ice slurry and preserved in 100% ethanol for subsequent determination of life-history traits.

Size, morphology, age and reproductive status

Preserved fish were weighed to the nearest 1 mg and the total length (TL) and standard length (SL) measured to the nearest 1 mm. Fish were then dissected, sexed and the gonads removed and weighed to the nearest 1 mg. The gonadosomatic index (GSI) (= gonad weight/body weight x 100) was calculated for a subsample of fish from both upper and lower catchment sites. Sample sizes for GSI studies from the upper catchment sites across months were n = 42 (October), n = 46 (November), n = 19 (February) and n = 33 (March); and for the lower catchment sites were n = 22 (October), n = 10 (November), n = 4 (December), n = 22 (February) and n = 43 (March). At the same time, gonads were assigned, on the basis of their morphological appearance, to one of the following seven maturity stages (Laevastu 1965): I-virgin; II-maturing virgin or recovering spent; III-developing; IV-developed; V-mature or gravid; VI-spawning; or VII-spent.

Sagittal otoliths are widely used to provide age estimates of various fish species, including atherinids (Campana 2001). The highly seasonal Mediterranean climatic regime in south-western Australia has resulted in most of the regions' freshwater fish species having otoliths with clearly defined annuli that are laid down once each year (Pen & Potter 1991; Morgan *et al.* 1995, 2000; Morgan 2003). Therefore, although previous age analysis for *L. wallacei* was based on length-frequency distributions (Prince & Potter 1983), we have provisionally assumed that otoliths are appropriate for ageing the fish in this study, although we note that the formation of annuli on the otoliths has not yet been validated for the species. The sagittal otoliths of each fish were removed, cleaned and stored in gelatin capsules. To count the number of translucent zones, they were later placed in methyl salicylate in a black dish and examined under a dissecting microscope at 40x magnification using reflected light. The approximate age of fish was calculated by using a birth date of 1st October for fish from the upper catchment and a birth date of 1st January assigned for fish from the lower catchment (see results for rationale). von Bertalanffy growth curves were then fitted to each of the fish at an estimated age from each of the upper and lower reaches of the catchment. These curves were fitted with SigmaPlot using the growth equation $L_t = L_\infty[1-e^{-K(t-t_0)}]$, where L_t is the length at age t (years), L_∞ is the asymptotic length, K is the growth coefficient, and t_0 is the hypothetical age at which the fish would have zero length. A likelihood ratio test (Cerrato 1990) was employed to determine whether the growth curves of *L. wallacei* differed between the upper and lower catchment.

Differences in sex ratio of fish populations between catchments were compared by Fisher exact test. The effect of sex and catchment region on fish TL was tested by a two-factor analysis of variance, while the effect of these variables on fish weight was tested by a two factor analysis of covariance, with TL as a covariate. All statistical tests were conducted in JMP v4 (SAS Institute, Cary, NC) and for parametric tests, variables were tested for normality and homogeneity of variances prior to analysis.

Dietary analysis

In order to determine the diet of *L. wallacei*, which lacks a stomach, the contents of the anterior half of the intestine were examined under a dissecting microscope. All matter was identified to the lowest possible taxonomic level using Davis & Christides (1997). Gut fullness was also estimated on a scale from 0 to 10, with 0 being an empty intestine, 8 being full and 10 being a fully distended intestine. Contents were analysed using the percentage frequency of occurrence and the percentage of volumetric contribution of each dietary item. The percentage frequency of occurrence is the proportion of the total number of guts that contain a particular prey type, while the percentage of volumetric contribution is the proportion of each prey type to the overall gut contents of each fish, calculated using the points method (Hynes 1950; Hyslop 1980).

Similarities in diet among individual fish were estimated from percentage volumetric data using the Bray-Curtis similarity coefficient (Bray & Curtis 1975). Percentage volumetric data were square root transformed prior to analysis to downweight the influence of dominant species. The significance of differences in diet among fish from different catchment areas or seasons was tested by a pseudo two-way analysis of variance procedure applied to the pairwise similarity matrix (PERMANOVA, implemented using the computer packages PRIMER 6.0 and PERMANOVA+; Clarke & Gorley 2006; Anderson *et al.* 2008). The contribution of individual prey items to the similarity within groups or the dissimilarity among groups was assessed by averaging the Bray-Curtis similarity (or dissimilarity) term for each species over all pairwise fish combinations, using the SIMPER procedure in PRIMER 6.0 (Clarke & Gorley 2006).

Fluctuating asymmetry

Fluctuating asymmetry (FA) is often used as an indicator of environmental stress during development (see Allenbach *et al.* 1999; Almeida *et al.* 2008). FA values were calculated from paired measurements of the number of fin rays on the right and left pectoral and pelvic fins, and length, width, perimeter and area of the right and left sagittal otoliths for each fish. Initially, directional asymmetry was tested by the skewness and anti-symmetry by the kurtosis of signed differences of right and left variable distributions. If the signed variable distributions were not significantly skewed, bimodal or platykurtic, FA was calculated as the unsigned difference between right and left measurements (this corresponds to the FA1 measure of Palmer (1994)).

Relationships between FA and character size were tested with Pearson product-moment correlations and differences in FA values between catchments, seasons, fish age classes and rates of parasitism were tested by analyses of variance. All statistical tests were conducted in JMP v4 (SAS Institute, Cary, NC). All variables were tested for normality and homogeneity of variances prior to analysis. Tests of differences in FA using different morphological variables were regarded as multiple tests of the same hypothesis, and therefore a Bonferroni correction was applied to ensure an experiment-wide error rate of 5%.

Parasitism

Parasitic organisms have recently been shown to be highly sensitive indicators of environmental stress and examining how parasite populations vary across environmental gradients may provide valuable information on the ecological impact of pollutants (Marcogliese 2005; Lafferty 2008). During morphological measurements and dissection, each fish was examined for macroparasites (helminths and arthropods) using methods described in Lymbery *et al.* (2010). All detected parasites were removed, photographed and then preserved in 70% ethanol. If necessary, specimens were cleared in lactophenol and prepared as whole mounts for microscopic identification. Parasite specimens were identified to the lowest taxon possible using standard taxonomic keys.

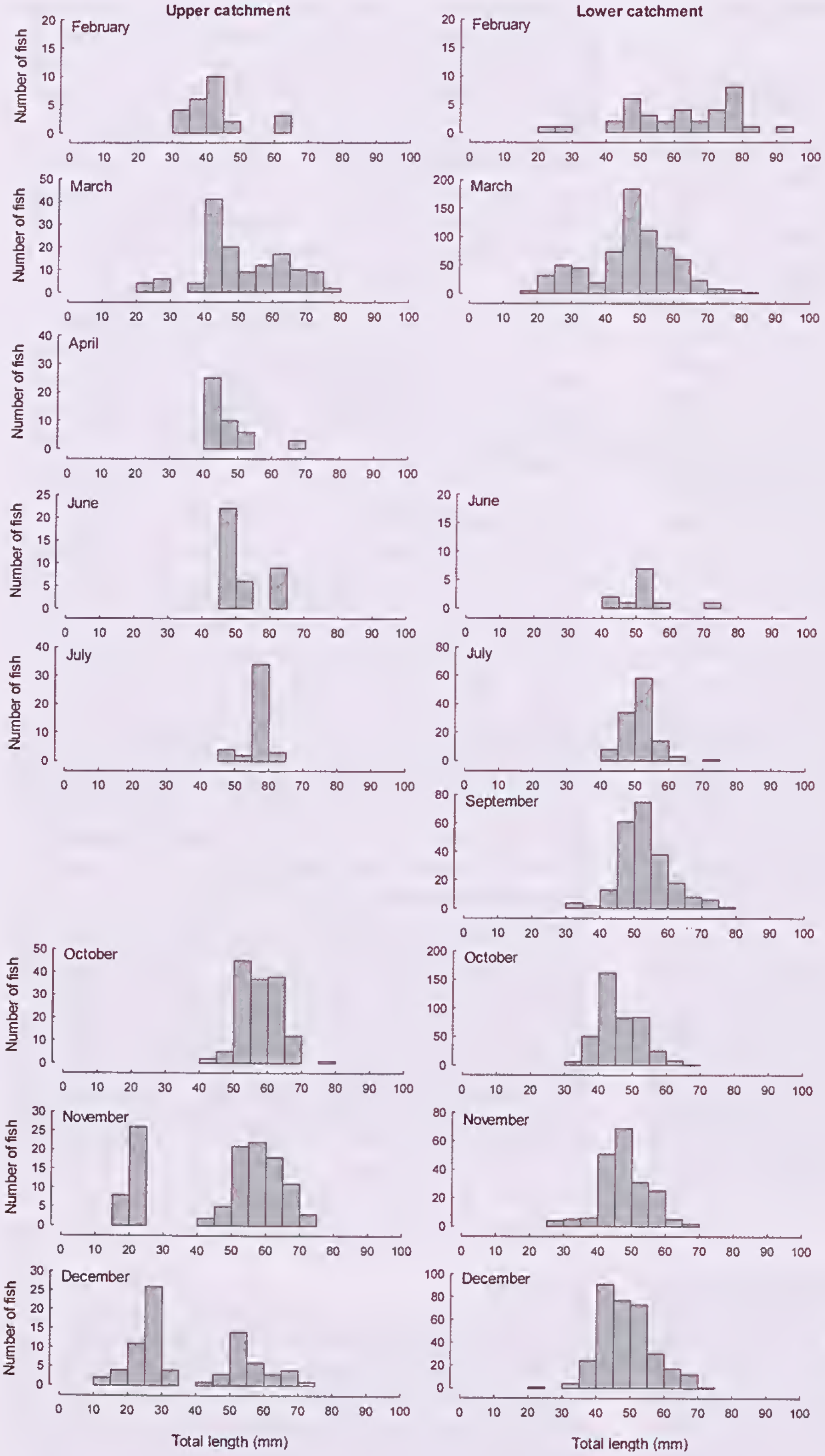

Figure 2 Length-frequency histograms of *Leptatherina wallacei* captured during this study from the upper (left) and lower (right) catchment of the Blackwood River.

From all fish sampled and for fish from different parts of the catchment (i.e. upper or lower) or seasons, the overall prevalence of parasitic infection (i.e. the proportion of fish infected with any species of parasite) as well as prevalence of each parasite species, with 95% confidence intervals calculated assuming a binomial distribution, were determined using the software Quantitative Parasitology 3.0 (Rózsa *et al.* 2000). Mean intensity (i.e. the number of parasites per infected fish), with 95% bootstrap confidence intervals, was also calculated for each parasite species using Quantitative Parasitology 3.0 (Rózsa *et al.* 2000). Differences in parasite prevalence among groups were investigated using Fisher exact tests and differences in mean intensity using the bootstrap.

RESULTS

Fish distribution

Leptatherina wallacei was found throughout the year in both main channel upper catchment and main channel lower catchment sites, but was never recorded from tributary sites. Over all sampling sites and times, *L. wallacei* was the second most abundant fish species found in the upper catchment, making up 14% of the total fish catch (total n = 11,798), while in the lower catchment it was the third most abundant species, making up 22% of the total fish catch (total n = 14,931). In addition to *L. wallacei*, three other fish species (the native estuarine species *Pseudogobius olorum*, the native freshwater *Galaxias occidentalis* and the alien *Gambusia holbrooki*) were found in upper catchment sites, while in addition to *P. olorum*, *G. occidentalis* and *G. holbrooki*, a number of other fish species (the native estuarine *Afurcagobius suppositus*, and the native freshwater *Bostockia porosa*, *Nannoperca vittata*, *Nannatherina balstoni* and *Tandanus bostocki*) were found in lower catchment sites.

Size, age and growth rates

Based on the number of translucent zones on the otoliths, *L. wallacei* of three different age classes (0+, 1+ or 2+) were found in the study; the largest fish being 90 mm TL and in its third year of life. From the von Bertalanffy growth equations (where L_∞ = 75.12 and 83.83 for fish from the upper and lower catchments, respectively, t_0 = -0.6785 and 0.1463, respectively and K = 0.9659 and 1.8335, respectively) on average, fish in the upper catchment attained ~60 mm TL at the end of their first year of life and ~69.5 mm TL at the end of their second year of life, while fish in the lower catchment attained ~66 and 81 mm TL at these respective ages. These growth curves were found to differ significantly ($p > 0.05$) between fish in the upper and lower catchments.

Over all sampling sites and dates, there was a strongly female-biased sex ratio (1.63 female: 1 male, n = 776). This was more pronounced in lower catchment sites than in upper catchment sites (73% versus 56% female; significantly different by Fisher exact test, p = 0.01). There was a strong positive relationship between TL and weight for both female and male fish. Fish TL was significantly affected by sex ($F_{1,772} = 16.33$, $p < 0.0001$), but not by position in the catchment ($F_{1,772} = 2.55$, $p = 0.11$) or the interaction of sex and catchment ($F_{1,772} = 0.34$, $p = 0.56$). Female fish (mean TL = 60.2 ± 0.6 mm) were, on average, longer than male fish (mean TL = 54.5 ± 1.2 mm). Fish weight, with length as a covariate, was significantly affected by position in the catchment ($F_{1,772} = 6.62$, $P = 0.01$), but not by sex or the interaction of sex and position in the catchment. Fish from lower catchment sites (mean weight = 1.11 ± 0.03g) were significantly heavier than fish from upper catchment sites (mean weight = 1.03 ± 0.01g).

The length-frequency distributions of *L. wallacei* showed different trends in upper and lower catchment sites (Figure 2). In the upper catchment, new recruits (15–24 mm TL) first appeared in late spring (November) and grew rapidly over summer to reach 40–44 mm TL by autumn (March). Large fish (>50 mm TL) persisted throughout the year but appeared to decline in number post spawning. By contrast, in lower catchment sites new recruits (<20 mm TL) were not detected until autumn (March) and appeared to grow slowly through winter and spring, with numbers in the 40–44 mm TL class peaking in October. There was no dramatic reduction in the numbers of large fish (>50 mm TL) after the appearance of these recruits.

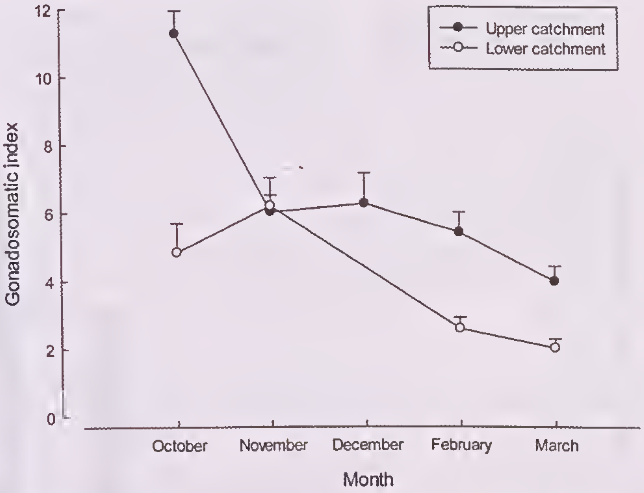

Figure 3 Gonadosomatic index (95% CI) of female *Leptatherina wallacei* from upper (black circles) and lower (white circles) catchment of the Blackwood River between mid-spring and early-autumn.

Gonadal development

There was a marked difference in the timing and extent of gonadal development between female fish in the upper and lower catchments. In upper catchment sites mean GSI's of female *L. wallacei* peaked in mid-spring when they reached 11.25, before declining to ~6.0 in both November and December, 5.4 in February, and 4.0 in March (Figure 3). In lower catchment sites mean GSI's peaked in November at 6.18, before declining to less than 3.0 in February and March (Figure 3). In comparing gonadal development stage between fish in mid-spring (October), those in the upper catchment were mature (stage V), spawning (stage VI) or spent (stage VII), while those in the lower catchment were developing or maturing, with less than 15% having attained maturity (stage V), and none had spawned or were spent (Figure 4). Spawning and spent fish were first recorded in the lower catchment in late summer and at this time fish in the upper catchment exhibited a full range of gonadal development stages, indicating that the spawning period is more protracted for fish in the upper catchment (Figure 4). The smallest total length at which a fish with stage VI or VII gonads was found, was 47 mm TL in the upper catchment and 48 mm TL in the lower catchment.

Fish diets

Leptatherina wallacei was found to be carnivorous, with a wide range of invertebrate taxa consumed (Table 1). The most common prey were of the insect orders Diptera and Trichoptera and the crustacean orders Amphipoda, Copepoda and Ostracoda. There was a significant effect of catchment ($F_{1,251} = 22.80$, $p = 0.001$), season ($F_{1,251} = 8.65$,

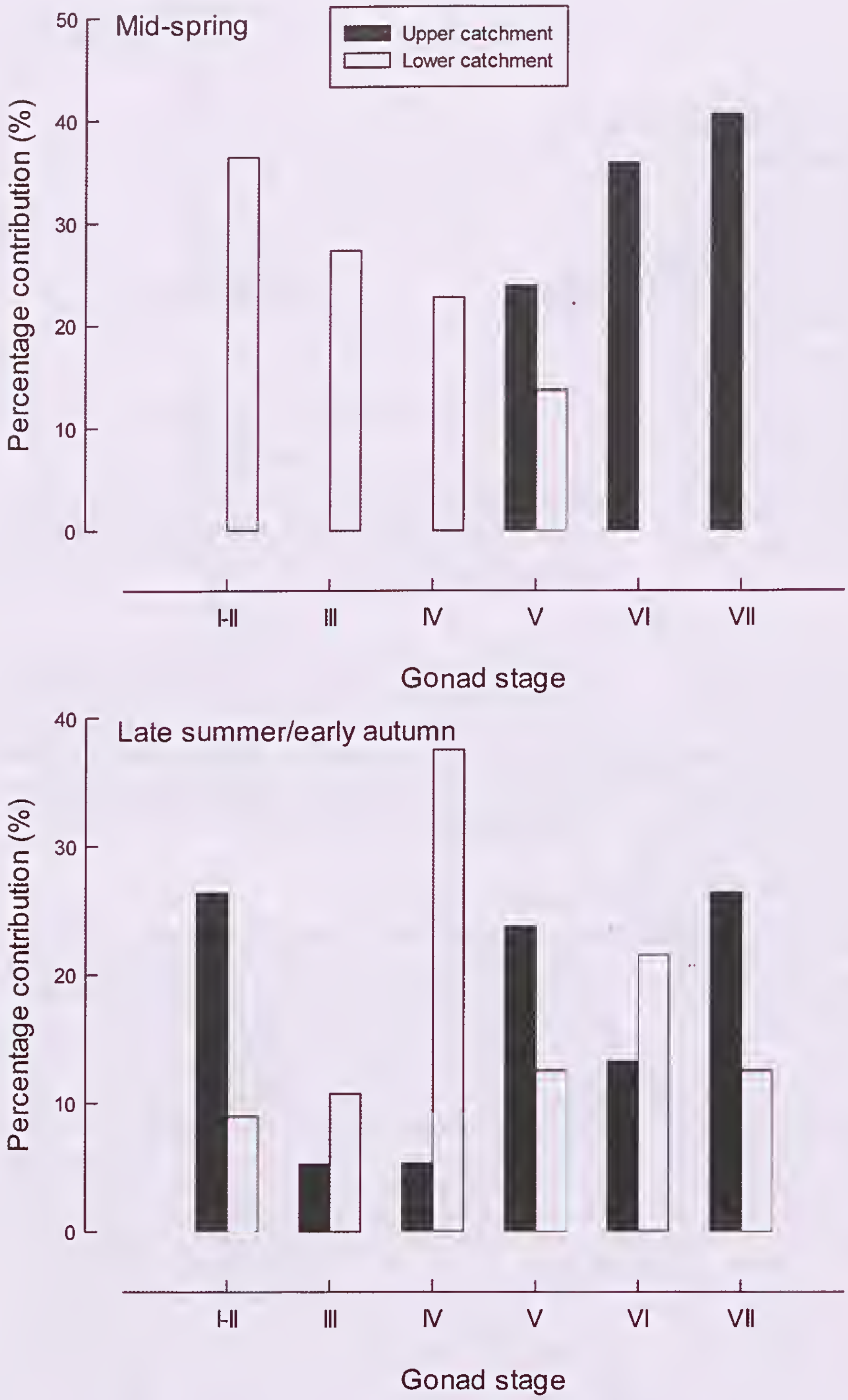

Figure 4 Percentage contributions of different gonadal stages for female *Leptatherina wallacei* from the upper (black bars) and lower (white bars) catchment of the Blackwood River in mid-spring and late summer/early autumn.

p = 0.001) and their interaction ($F_{1,251}$ = 5.22, p = 0.001) on prey consumed. SIMPER analysis found that in the dry season, 75% of differences in diet between fish in different parts of the catchment were explained by a relatively greater abundance of trichopteran larvae and hymenopterans in the diets of fish from lower catchment sites, and a relatively greater abundance of dipteran larvae, amphipods and ostracods in the diets of fish from upper catchment sites (Table 2). In the wet season, almost 90% of the differences between catchments were explained by a greater abundance of trichopteran adults and larvae, and dipteran larvae in the diets of fish from lower catchment sites, and a relatively greater abundance of amphipods and copepods in the diets of fish from upper catchment sites (Tables 1, 2).

Fluctuating asymmetry

All fin and otolith traits were variable, with ranges of 11–13 for pectoral fin ray number, 5–6 for pelvic fin ray number, 1.6–2.2 mm for otolith length, 1.4–2 mm for otolith width, 2.5–4.1 mm^2 for otolith perimeter and 2–2.8 mm for otolith area. The distributions of all right-left

Table 1 Proportional contribution (by volume) of different prey taxa in the diet of *Leptatherina wallacei* from the upper and lower catchment of the Blackwood River in wet and dry seasons.

Prey type	Upper catchment		Lower catchment	
	Dry season (n = 128)	Wet season (n = 73)	Dry season (n = 47)	Wet season (n = 23)
Amphipoda	0.21	0.26	–	–
Ostracoda	0.21	0.05	–	–
Copepoda	0.06	0.24	–	0.06
Cladocera	0.06	0.01	–	0.02
Diptera larvae	0.35	0.39	0.11	0.41
Diptera adults	0.06	0.03	0.06	0.04
Hymenoptera	–	–	0.12	–
Coleoptera larvae	–	0.01	0.04	–
Coleoptera adults	0.02	–	0.09	–
Odonata	0.01	–	–	–
Trichoptera larvae	0.02	–	0.54	0.26
Trichoptera adults	–	–	–	0.19
Ephemeroptera	–	–	–	0.01
Arachnida	–	–	0.02	–
Decapoda	0.06	–	–	–
Fish larvae	0.02	–	–	–
Plant material	–	–	0.02	–

Table 2 Mean abundance of different prey taxa in the diet of *Leptatherina wallacei* from upper and lower catchment sites in each season, and cumulative percentage of dissimilarity between these site explained by these taxa (calculated from one-way SIMPER analyses, because of significant interaction between catchment and season). Taxa are arranged in order of decreasing contribution to dissimilarity, and taxa which contributed less than 1% to the cumulative percentage of dissimilarity have been omitted.

Prey type	Mean abundance		Cumulative % dissimilarity
	Upper catchment	Lower catchment	
Dry season			
Trichoptera larvae	0.02	0.54	28.9
Diptera larvae	0.35	0.11	49.2
Amphipoda	0.21	–	60.3
Ostracoda	0.17	–	69.1
Hymenoptera	–	0.12	75.3
Diptera adults	0.06	0.02	81.3
Coleoptera adults	0.06	–	86.9
Cladocera	0.02	0.01	90.3
Wet season			
Diptera larvae	0.39	0.41	29.0
Amphipoda	0.26	–	45.2
Copepoda	0.24	0.06	61.4
Trichoptera larvae	–	0.26	77.4
Trichoptera adults	–	0.19	89.2
Diptera adults	0.03	0.04	93.6
Ostracoda	0.05	–	96.6
Cladocera	0.01	0.02	98.5

difference values for fins and otolith traits were not significantly skewed and were all slightly leptokurtic, indicating that they were not directionally symmetric or anti-symmetric. FA values were therefore calculated for all traits and in no case were FA values significantly correlated with trait size. There were no significant differences in FA for any trait between sexes, between adult and juvenile fish, between fish infected or not infected with parasites (see below), between fish sampled in wet and dry seasons or between fish from upper catchment and lower catchment sites.

Parasite fauna

Four species of endoparasitic helminths (three nematodes and a trematode) were found in *L. wallacei*, with an overall prevalence of parasitic infection (i.e. infection with any species of parasite) of 0.06 (n = 333). All of the helminth parasites were larvae. Of the nematodes, a species of *Eustrongylides* (possibly *Eustrongylides gadopsis*) was found in the abdominal cavity, a species of *Contracaecum* was found in the abdominal cavity, liver and ovaries, and a third, unidentified species of nematode was found in the gastrointestinal tract. Metacercariae of *Diplostomum* sp. (possibly *Diplostomum galaxiae*) were found in the skin and internal organs.

Significantly more fish were infected with parasites in lower catchment sites than in upper catchment sites (overall prevalence of infection of 0.14 compared to 0.03, Fisher exact test, $p < 0.001$) (Table 3). There were no significant differences in mean intensity of parasites between the upper and lower catchment for any species, but prevalences of *Contracaecum* sp. and the unknown species of nematode were significantly greater in fish from lower catchment sites than in fish from upper catchment sites (Table 3; Fisher exact test, $p < 0.01$ for both parasite species).

DISCUSSION

Distribution

Leptatherina wallacei is widely distributed in the south of Western Australia (Morgan *et al.* 1998). It is absent from marine environments and has historically been most often associated with upper estuaries, extending into

Table 3 Prevalence and mean intensities of infection (with 95% confidence intervals in parentheses) of parasite species found in *Leptatherina wallacei* sampled from sites in the upper catchment and lower catchment of the Blackwood River.

Parasite species	Upper catchment		Lower catchment	
	Prevalence	Intensity	Prevalence	Intensity
Eustrongylides	0.013 (0.004-0.038)	1	0.020 (0.004-0.073)	1
Contracaecum	0.009 (0.002-0.031)	1	0.070 (0.033-0.139)	3.71 (1-9.00)
Unknown nematode sp.	0.004 (0.001-0.025)	1	0.050 (0.020-0.113)	3 (1.4-5.8)
Diplostomum	–	–	0.030 (0.008-0.084)	1

the lower reaches of associated rivers (Prince *et al.* 1982; Prince & Potter 1983; Valesini *et al.* 1997; Morgan *et al.* 1998). The current study found that *L. wallacei* was most abundant throughout the upper catchment of the Blackwood River, occurred at lower abundance in the main channel of the lower catchment, and was absent from lower catchment tributaries. This supports the distribution and abundance of the species previously reported in the Blackwood River and other salinised rivers in the south-west of Western Australia (Morgan *et al.* 1998, 2003; Beatty *et al.* 2008). It has been hypothesised that the reversal of the typical longitudinal salinity gradient in many rivers in the south-west (i.e. increasing salinity with increasing distance from the ocean) has facilitated the upstream movement of estuarine fishes, such as *L. wallacei*, where they replace salt-sensitive freshwater fishes (Morgan *et al.* 2003; Beatty *et al.* 2010). Although *L. wallacei* is sympatric with six native and two introduced freshwater fish species in the lower catchment of the Blackwood River, the only other species found in the upper catchment are the native freshwater species *G. occidentalis*, the native estuarine/occasional freshwater species *P. olorum* and the alien freshwater species *G. holbrooki*.

Whether the greater relative abundance of *L. wallacei* in the upper catchment of the Blackwood River is a direct consequence of increased salinity *per se*, or of other abiotic or biotic factors, is not something that can be definitively determined from our study. One of the problems with inferring the effects of salinisation on freshwater organisms from field observations is that salinity is likely to covary with other environmental factors, thereby making it difficult to attribute salinity as the direct cause of distributional changes. There is a need for experimental studies, such as determining the salinity tolerance of *L. wallacei*, so that the effects of salinity can be separated from other factors. Although the precise salinity tolerance of *L. wallacei* has not been investigated, there is some information on upper and lower tolerance levels. Thompson & Withers (1992) found that *L. wallacei* could survive in salinities of up to 85 ppt for at least seven days in the laboratory, while in the field Morgan *et al.* (1998, 2003) have found *L. wallacei* at salinities from <1 ppt up to 38 ppt and Beatty *et al.* (2008) reported spawning at salinities as low as 1–2 ppt.

Life-cycle

The life-cycle of *L. wallacei* in the Blackwood River could be most clearly determined in the upper catchment. It appears that in the upper catchment, *L. wallacei* typically survives for just over one year, with spawning occurring in spring followed by some mortality of adults. The presence of some fish with significantly greater lengths than 0+ cohorts, and with one or two translucent zones on their otoliths, indicates that these individuals can survive well into their second or even third year of life, although this interpretation should be treated cautiously until the counting of otolith annuli is validated for determining age in this species. An annual life-cycle with spring spawning of *L. wallacei* in the upper catchment of the Blackwood River is consistent with that reported for an estuarine population in the Swan-Avon river system by Prince & Potter (1983). The life-cycles of three other species of Atherinidae (*Atherinosoma presbyteroides*, *Atherinosoma elongata* and *Allanetta* (*Craterocephalus*) *mugiloides*) in the Swan-Avon River system were also investigated by Prince & Potter (1983) and they found that all of these species typically have a one year life-cycle, as is also common for many Northern Hemisphere atherinids (e.g. Nelson 1968; Davis & Louder 1969; Henderson & Bamber 1987; Huber & Bengtson 1999).

In the lower catchment of the Blackwood River, *L. wallacei* appeared to have a delayed and shorter spawning period and a much reduced reproductive output compared to the upper catchment. Peak GSI values were markedly less in fish from the lower catchment, and these fish were also significantly heavier than fish from upper catchment sites and attained larger sizes at the end of their first and second year of life; this is consistent with reduced reproductive effort because energy goes first into reproduction in fishes with short life-cycles (Henderson & Bamber 1987). Fish appeared to spawn in early summer in the lower catchment, and the post-spawning mortality of adults was not as marked as in the upper catchment. Although there have been no previous comparative studies of different populations of *L. wallacei*, other atherinids have been shown to have phenotypically plastic reproductive strategies, presumably as an adaptation to the variable environmental conditions experienced in estuaries (Henderson & Bamber 1987; Huber & Bengtson 1999).

The reduced reproductive activity and atypical life-cycle of *L. wallacei* in the lower catchment of the Blackwood River, compared to upper catchment and estuarine populations (Prince & Potter 1983), may be due to a number of causes. First, the lower salinities in this part of the river may place the fish under physiological stress. Fluctuating asymmetry is often used as a measure of developmental instability in fishes and other organisms, reflecting the inability of individuals to maintain homeostasis when faced with environmental stresses during development (Somarakis *et al.* 1997; Panfili *et al.* 2005; Almeida *et al.* 2008). Although there was no evidence of fluctuating asymmetry in *L. wallacei* from the lower catchment, we do not know the developmental history of these fish. Second, even if fish are not under physiological stress, there may be differences in environmental requirements for spawning between upper and lower catchment populations. For example (in addition to salinity) water temperatures, dietary items and rates of parasitism also differ between upper and lower catchments and these differences may impact on gonadal development rates (Pollard 1974; Morgan 2003).

Diet

This study found *L. wallacei* to heavily rely on a range of aquatic invertebrates or certain life-history stages of terrestrial insects, with only a very small portion of plant material consumed. This result is similar to previous research on the diet of many different atherinid species, including *L. wallacei*, in the south-west of Western Australia, showing that they are opportunistic feeders that consume benthic crustaceans, polychaetes, planktonic crustaceans and small amounts of detritus and plant material (Prince *et al.* 1982; Humphries 1993). Regardless of the season and location, dipteran larvae made important contributions in terms of number and volume to the diet. Despite the preponderance of dipteran larvae in the diet of all populations of fish in the Blackwood River, there were also important differences in diet between fish from upper catchment and lower catchment sites. Trichopteran larvae and adults were major contributors to the diets of fish from the lower catchment, but not to the diets of fish from the upper catchment. By contrast, fish from the upper catchment had a much greater proportion of crustaceans, particularly amphipods, ostracods and copepods, in their diet than did fish from the lower catchment. These differences most likely reflect differences in the invertebrate composition in different parts of the river, because of differences among invertebrate groups in salinity tolerance. Trichopterans, for example, are very salt-sensitive (Hart *et al.* 1991), and Bunn & Davies (1992) recorded a shift from insect dominated to crustacean dominated aquatic fauna in the river systems of south-western Australia as salinity increased. Hart *et al.* (1991) described crustaceans as the most salt-tolerant of the Australian aquatic macroinvertebrates.

Along with changes in salinity directly impacting invertebrate prey availability due to the relative salinity tolerances of those taxa, secondary salinisation may also indirectly impact invertebrate communities. While there is little information about the response of Australian freshwater algae or plant species toward environmental degradation, the majority of taxa do not appear to be tolerant of increasing salinity, with adverse effects on growth or reproductive ability appearing at salinities above 1 ppt (Nielsen *et al.* 2003b). Algae and aquatic plants do not form a major proportion of the diet of freshwater fishes in south-west of Western Australia (Morgan *et al.* 1998), so their elimination by rising salinity is unlikely to directly affect the growth rate of native fishes. However, there may be indirect effects of their loss by reducing food availability of herbivorous micro- and macroinvertebrates.

Parasites

In this study three species of parasitic nematode (*Contracaecum* sp., *Eustrongylides* sp. and an unidentified species) and one species of trematode (*Diplostomum* sp.) were found in *L. wallacei* in the Blackwood River. All of these parasites were present as larval stages, and use fishes as intermediate hosts in their life-cycle. The most prevalent parasite was *Contracaecum* sp. Species of *Contracaecum* have been previously reported in both estuarine and freshwater fishes in the south-west of Western Australia (Lymbery *et al.* 2002; Chapman *et al.* 2006). In the current study, many internal organs were infected with *Contracaecum*, principally the liver, but also the ovaries, which may cause infertility in the host.

Infections with *Contracaecum* and with the unidentified species of nematode were much more prevalent in *L. wallacei* from the lower catchment than in fish from the upper catchment. We hypothesise that this may be due to differences in salinity between these sites. Parasite populations are often adversely affected by human-induced environmental changes (Lafferty 1997; Tinsley 2005; Lymbery *et al.* 2010), and the present study appears to reinforce this finding. Most previous studies of environmental impacts on the parasites of fishes have been concerned with the effects of industrial pollution, eutrophication and acidification, and the effects of secondary salinisation have rarely been studied (although see Rogowski & Stockwell 2006). The reduced prevalence of parasites at higher salinities may reflect differences in the survival of free-living parasite stages, differences in the abundance of hosts or differences in transmission efficiency to hosts in different parts of the river. Without knowing the details of the life-cycle of the parasites, it is difficult to distinguish between these possibilities. Species of *Contracaecum* typically use invertebrates as a first intermediate host, fishes as a second intermediate host and piscivorous birds as a definitive host (Lymbery *et al.* 2002). Previous studies have found that piscivorous birds are less abundant in salinised rivers (Halse *et al.* 2003), and this may account for reduced rates of parasitism in the upper catchment sites. However, it may also be likely that the difference found for *L. wallacei* reflects a component of transmission efficiency that is peculiar to this species, such as a reduced consumption of the intermediate host(s) by *L. wallacei* populations in the upper catchment.

Regardless of the reason for the difference in parasite prevalence between populations of *L. wallacei* in the upper and lower catchments, it may have an impact on the relative ecological success of the species in these two areas. It has been suggested that reduced parasite load improves the demographic performance and competitive ability of alien species invading a new area (Torchin *et al.* 2002, 2003), although empirical data to support this are rare. Of particular interest in the current study is the greater prevalence in the lower catchment of *Contracaecum* sp., found in the internal organs, including the ovaries of infected fish. Whether this is a contributing factor to the apparent reduction in reproductive activity in this population is a question that deserves further study.

CONCLUSIONS

Secondary salinisation is a growing problem in the Southwestern Province and an increasing number of studies suggest that it, along with climate change (Beatty *et al.* 2014), is the greatest threat for the endemic freshwater fish species in this area (Morgan *et al.* 2003; Beatty *et al.* 2008, 2010, 2011). Not all fish species may be adversely affected by increasing salinity, however; in the case of *L. wallacei*, which is typically found within estuarine environments and a few coastal lakes, increasing salinity in the headwaters of the Blackwood River may have facilitated further inland penetration. The results of the study supports our hypothesis that there would be plasticity in key ecological traits of *L. wallacei* that may help explain why it is now the second most abundant fish in the upper catchment of the Blackwood River. It appears that increasing salinisation may improve the prospects for survival and spread of *L. wallacei* in the Blackwood River, because the life-cycle and diet of upper catchment populations are more similar to those of estuarine populations than they are to those of lower catchment populations. In addition, populations of *L. wallacei* in the upper catchment have reduced rates of parasitism, possibly because of the effects of salinisation on other parasite hosts.

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Prediction of potentially significant fish harvest using metrics of accessibility in northern Western Australia

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Management of freshwater fisheries in northern Australia faces challenges that combine Aboriginal and recreational harvests, intermittent river flows and remote, expansive management jurisdictions. Using relationships between fishing pressure (vis-à-vis 'accessibility') and the abundance of fish species targeted by Aboriginal and recreational fishers (derived from the Fitzroy River, Western Australia), the potential fishing pressure in subcatchments across the entire Kimberley region was assessed. In addition to the Fitzroy and Ord River, known to experience substantial fishing pressure, this assessment identified that subcatchments in the Lennard and King Edward river basins were also likely to experience relatively high fishing activity. Management of freshwater fisheries in the Kimberley region prioritises aquatic assets at most risk from the potential impact of all aquatic resource use and employs barramundi (*Lates calcarifer*) and silver cobbler (*Neoarius midgleyi*) as indicator species to track changes in their condition. Extending the existing monitoring of these indicator species (currently undertaken in the Ord and Fitzroy rivers) to include popular fishing areas in subcatchments of the Lennard and King Edward river basins will provide a better understanding of the current fishing pressure and its impact on the fisheries resource in the Kimberley region, as well as confirmation of the proposed method's predictive capability for this region. The ability to predict those areas that may experience increased fishing pressure in the future, offers an opportunity for the early monitoring and detection of any changes in the fisheries resource.

KEYWORDS: fisheries management, customary harvest, recreational fishing, Kimberley, intermittent rivers

INTRODUCTION

Rivers of northern Australia support high-value customary and recreational fish stocks (Toussaint *et al.* 2005; Pannell 2010; Toussaint 2010, 2014; Morgan *et al.* 2011; Jackson *et al.* 2012; Close *et al.* 2014). Fish contribute significantly to both Aboriginal household budgets, by providing an important food source for general consumption and during ceremonial events (e.g. Toussaint 2014), and the regional tourism-based economy (Altman 1987; Carson *et al.* 2009). Management of these fisheries faces a unique set of challenges that combine Aboriginal and recreational harvest (Jackson *et al.* 2012; Close *et al.* 2014; Toussaint 2014), intermittent river flows that restrict fish to disconnected refugia (Magoulick & Kobza 2003; Bunn *et al.* 2006; Carini *et al.* 2006; Beesley & Prince 2010; Sheldon *et al.* 2010) and remote, expansive management jurisdictions (Dale *et al.* 2014).

In Western Australia, the Department of Fisheries applies an Ecosystem Based Fisheries Management (EBFM) approach to assess the sustainability of fish stocks and determine the priorities for resourcing within six bioregions (DoF 2011). The EBFM approach acknowledges the links between fished resources and habitat, and through the Finfish Resource Assessment Framework (DoF 2011) indicator species are identified and monitored; the status of these indicators is assumed to represent the status of the resource (asset). The Kimberley region is incorporated into the North Coast and Northern Inland Bioregions for which barramundi *Lates calcarifer* (Bloch 1790) and silver cobbler *Neoarius midgleyi* (Kailola & Pierce 1988) are recognised as indicator species, and the risk of aquatic resource use to the sustainability of 'sooty grunter' (in the Kimberley region = Jenkins' grunter or western sooty grunter, *Hephaestus jenkinsi* (Whitley 1945)) is considered relatively high (DoF 2011). Within the Northern Inland Bioregion, Lake Argyle supports Western Australia's only commercial freshwater fishery, and recreational fisheries for barramundi and cherabin *Macrobrachium rosenbergii* (De Man 1879) are also included in the EBFM for this Bioregion (Newman *et al.* 2013).

Recent research conducted in the Kimberley region of north western Australia suggested that significant overlap/sharing of the fisheries resource exists between Aboriginal and recreational fishers, especially of targeted species including barramundi and Jenkins' grunter (Toussaint 2010; Jackson *et al.* 2012; Close *et al.* 2014). As noted by Close *et al.* (2014), the distinction between recreational and customary harvest is imprecise. Aboriginal people will fish for both recreational purposes as well as those inspired by customary law and practice. In some areas fishing sites are also shared, particularly in the Fitzroy River catchment where most fishing activities (both Aboriginal and recreational) are concentrated in permanent river pools of the main river channel (Jackson *et al.* 2012; Close *et al.* 2014). This concentration of fishing pressure at easily accessible sites has the potential to reduce the abundance of target species, especially

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barramundi and Jenkins' grunter (Close *et al.* 2014), species commonly used as bait (e.g. bony bream *Nematalosa erebi* (Günther 1868) and spangled perch *Leiopotherapon unicolor* (Günther 1859)) to catch larger predatory species, and sawfish *Pristis pristis* (Linnaeus 1758), which are targeted by Aboriginal fishers and regularly caught (but not targeted) by recreational fishers (Thorburn *et al.* 2007; Morgan *et al.* 2011).

Tourism and recreational activities (amongst other disturbances) have been identified as potential threats to the sustainability of rivers in northern Australia (e.g. Pusey 2011). The potential for over-exploitation of fisheries resources is likely to be a major consequence of this threat (Pusey *et al.* 2004; Pusey & Kennard 2009; Close *et al.* 2014). Although current regulations govern harvest of fish by Aboriginal and recreational fishers in Western Australia (see Close *et al.* 2014), compliance with these regulations is only monitored during the peak tourism period between May and October in the Fitzroy and Ord rivers, due to the seasonal access and the high number of campers and fishers that visit these areas, and because these catchments are known to be important breeding areas for barramundi. Early detection of any changes in the fisheries resource may be enhanced if those areas currently subjected to high fishing pressure, or likely to experience significant fishing pressure in the future, can be predicted.

Using relationships derived from the Fitzroy River, Western Australia, between fishing pressure (vis-à-vis 'accessibility') and the abundance of fish species targeted by Aboriginal and recreational fishers (Close *et al.* 2014), we provide a preliminary assessment of potential fishing pressure across the entire Kimberley region. In the absence of any comprehensive alternative data, we also provide a simple comparison of those subcatchments predicted to experience significant fishing pressure, with those known to be popular with fishers across the region. We briefly discuss the implications of these results for ecosystem-based fisheries management currently implemented across the Kimberley region.

METHODS

The Kimberley region of Western Australia covers 425 000 km², and is bounded by the Indian Ocean in the north-west, the Northern Territory in the east and the Great Sandy Desert in the south. The region includes 10 major drainage basins (Figure 1) within the Kimberley and Northern provinces defined by Unmack (2013) and based on the biogeography of Australian freshwater fishes. Those river basins in the Kimberley Province include the Fitzroy, Keep, Drysdale, Prince Regent, Isdell, King Edward and Lennard. The Pentecost and Ord river basins form the western most extent of the Northern Province, which extends east to approximately Cairns and includes all river basins draining northern Australia, including the Wet Tropics Region of Far North Queensland. The Cape Leveque Coast basin, which contains no large rivers, overlaps the boundary between the Kimberley Province (to the east) and the Paleo Province (to the west).

The Kimberley contains six major population centres: Kununurra and Wyndham in the north east, and Halls Creek, Fitzroy Crossing, Derby and Broome in the south and west (Figure 2). There are only two main transport routes within the region, the Great Northern Highway (GNH) and the Gibb River Road (GRR) that traverse the Kimberley from east to west (Figure 2). An additional two transport routes provide access during the dry season to Kalumburu and the Dampier Peninsula via the GRR and the GNH respectively (Figure 2). The GNH traverses the Fitzroy River basin crossing, or running close to, the lower and middle reaches of the Fitzroy River, the lower reaches of the Margaret River and mid

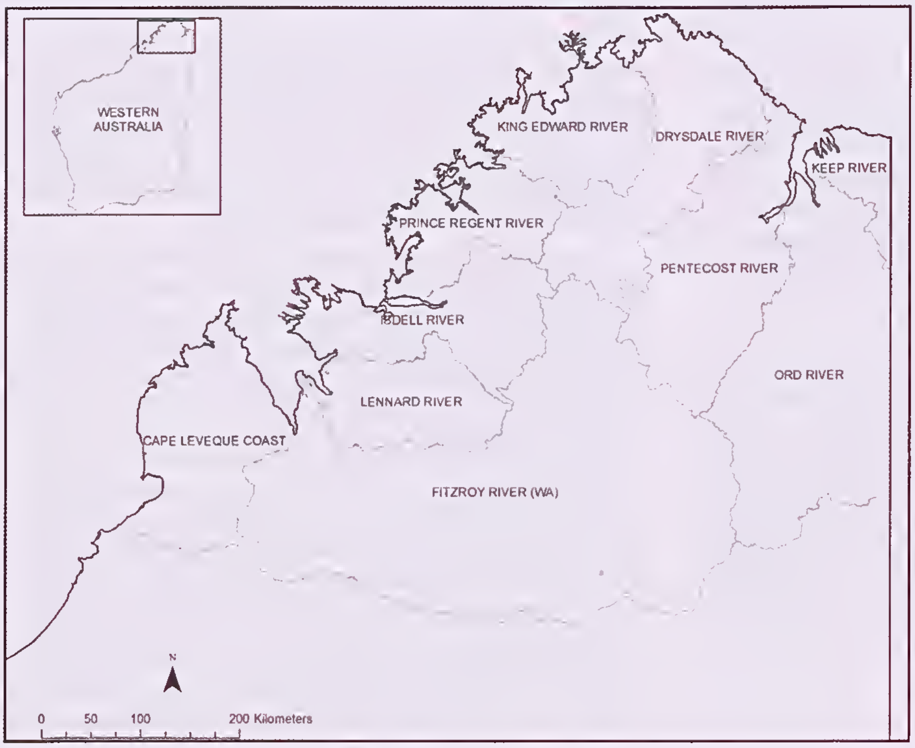

Figure 1 Major river basins in the Kimberley region of northern Western Australia.

reaches of the Mary River. It also provides access to the Ord River basin (Dunham River, upper and lower Ord River). The GRR passes through approximately 180 km of the Lennard River catchment and crosses through the Pentecost River basin providing access to the Pentecost, Durack and Chamberlain rivers and their tributaries. Unsealed over much of its length, the GRR is closed for most of the wet season, except for all-weather sections at either end, which provide access to the Pentecost River from the east and the May River from the west for most of the year. The road to Kalumburu passes through the centre of the King Edward River catchment and also provides access to the Drysdale River during the dry season only. The Cape Leveque Road provides access to coastal waters.

Approximately 40% of the region's population is Aboriginal (ABS 2011). Major communities (populations of over 50 people) (Figure 3) are distributed: in the west

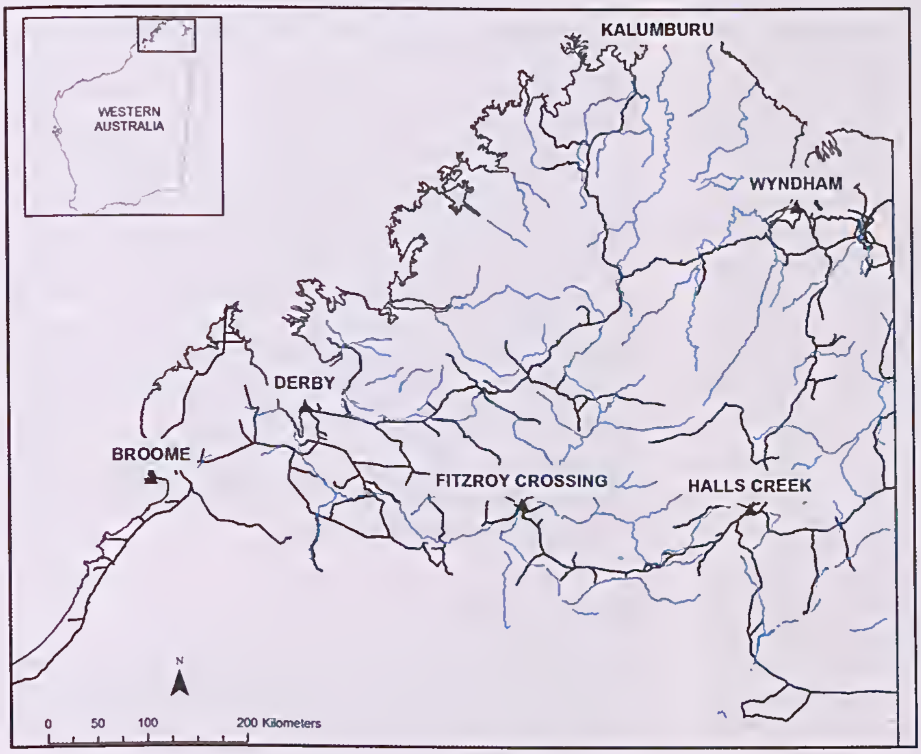

Figure 2 Rivers (——), roads (——), and major population centres (▲) in the Kimberley region of northern Western Australia.

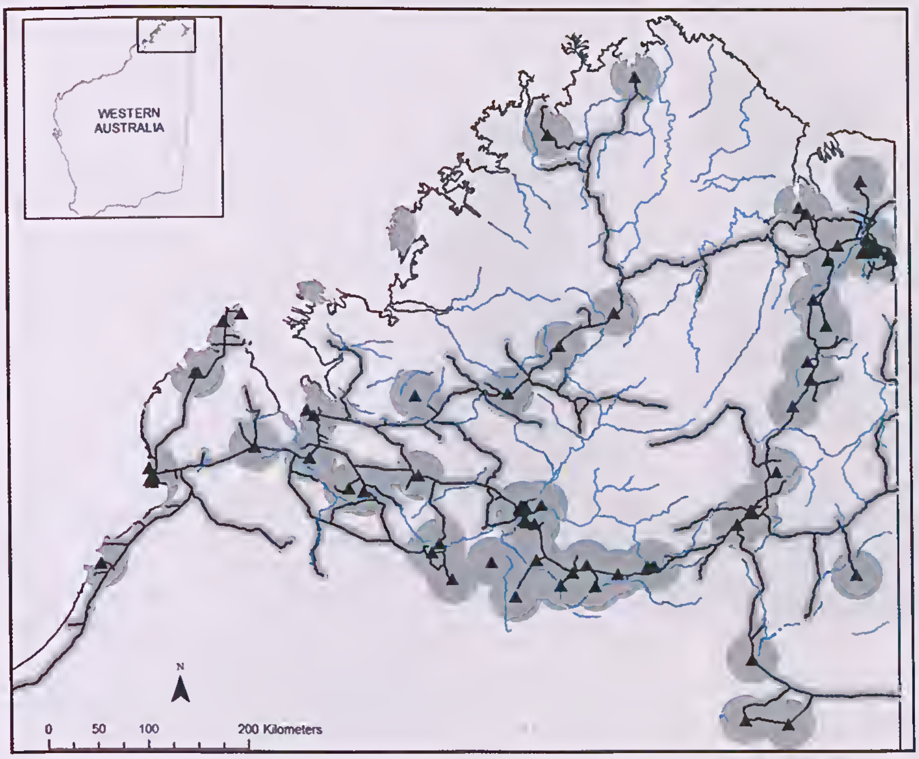

Figure 3 The distribution of 'accessible' areas (▨), based on proximity to regional towns, Aboriginal communities (▲), roads and road crossings, that are likely to experience high fishing pressure.

along the GNH (Fitzroy River), the GRR and on the Dampier Peninsula; in the east around Halls Creek and the Ord River; and in the North around Kalumburu.

Four metrics of accessibility, which infer the potential combined Aboriginal and recreational 'fishing pressure', were quantified using GIS (Graphical Information Software; Arcmap V10): linear distance to the nearest road, river distance to nearest road crossing, linear distance to nearest community, and road distance to nearest regional town. These metrics were identified by Close *et al.* (2014) as suitable metrics to quantify fishing pressure. To model potential fishing pressure across the Kimberley region, these metrics were mapped using GIS by applying a 25km buffer around population centres and a 5km buffer either side of roads (following Close *et al.* 2014; Figure 3). These buffers provide a map of 'accessibility' across the region (areas within the buffer were considered accessible and those outside were considered inaccessible). The percentage of 'accessible' river length within subcatchments was then calculated. This method assumes that the relationship between fishing pressure and abundance of targeted species developed from the Fitzroy River (Close *et al.* 2014) is applicable across the region. This is considered justifiable as most rivers in the region share the same targeted freshwater fish as those in the Fitzroy River (Morgan *et al.* 2011).

RESULTS

The spatial analysis of accessibility metrics (Figure 4) indicates subcatchments where accessibility to the river channel may potentially result in increased fishing pressure. River basins (*c.f.* Figure 1) that contain subcatchments with relatively high accessibility include the Fitzroy, Lennard and Isdell river basins in the west Kimberley, the King Edward River basin in the north Kimberley and the Ord and Keep river basins in the east Kimberley (Figure 4). The Cape Leveque Coast basin is also identified as highly accessible, however, as there are no major rivers in this area and the abundance of targeted species is very low (unpublished data), fishing activity targeting freshwater species is presumed low. In all other river basins (*c.f.* Figure 1) spatial analysis predicted that accessibility to major river channels is limited (Figure 4).

In the Fitzroy River basin, the lower reaches of the Fitzroy River downstream of Fitzroy Crossing, the Margaret River, as well as the Mary River are accessible. Upstream of Fitzroy Crossing, accessibility to the main drainages including the O'Donnell, Leopold and Fitzroy rivers is limited, except in the basin's upper most reaches where sections of the Hann River can be accessed. Most of the Lennard River basin, including the May, Lennard and Barker river subcatchments are accessible with exception of the Broome Creek subcatchment. Most of the Isdell River basin is difficult to access, with the exception of the upper reaches of the Isdell River and its tributaries. Most of the King Edward River basin is accessible, especially the upper reaches of the King Edward River, Mitchell River, Camp Creek and the mid-lower reaches of the Carson River. Most of the Western Australian part of the Ord River Basin is accessible, especially downstream of Lake Argyle. Similarly, river reaches of the Keep River basin within Western Australia are identified as being accessible.

DISCUSSION

Overexploitation in freshwater fisheries is largely unrecognised (compared to marine fisheries), poorly documented and, because fishery declines are often

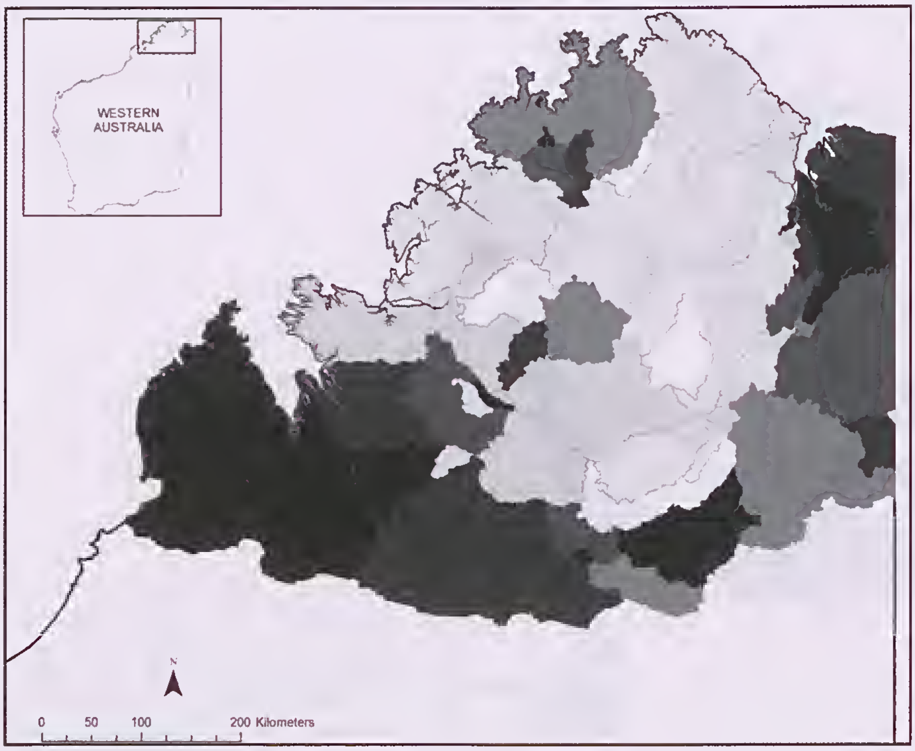

Figure 4 The likely fishing pressure in subcatchments, based on the percentage of 'accessible' river length within each subcatchment. Shading depicts an arbitrary gradient from accessible sites with potentially high fish pressure (black) to inaccessible sites with potentially low fishing pressure (no shading).

confounded with other pressures such as habitat loss and environmental degradation, the effects on sustainability remain poorly understood (Cooke & Cowx 2004; Allan *et al.* 2005). Considering the limited anthropogenic disturbance in the Kimberley region (Stein *et al.* 2002; *c.f.* Vörösmarty *et al.* 2010), there is an opportunity to compile comprehensive baseline data on the current state of local fisheries and investigate potential monitoring programs to detect any changes in habitat availability and fish abundance at appropriate scales for management, policy development and regional knowledge.

Such information is likely to benefit management of freshwater fisheries across the Kimberley (and other regions of northern Australia) as the extent of the region's river channels that are subject to concentrated fishing pressure (such as increasing numbers of recreational fishers) is likely to increase as the region becomes more accessible (due to infrastructure, i.e. road networks, and increased tourism ventures including helifishing and luxury cruise boats that are already accessing freshwater systems via the coastline). The effect of fishing on the abundance of targeted species may also increase, especially in systems where climate-related changes to groundwater recharge may reduce the number, persistence and/or size of permanently watered river pools that provide dry-season refugia for those species harvested (see Close *et al.* 2014).

Monitoring of fisheries resources in the Kimberley and compliance of fishers to regulations is problematic. In the absence of any available data, evidence supporting the predictions of river reaches subject to potentially high fishing pressure is limited to 'local knowledge'. In general, our predictions are consistent with those areas known anecdotally to be popular with Aboriginal and/or recreational fishers. In contrast, although the Pentecost river basin was shown to have limited accessibility (Figure 4), the Pentecost and Chamberlain rivers are popular fishing places for Kimberley locals and tourists. Conversely, the Keep River Basin showed high accessibility, but there is known to be limited fishing in the smaller coastal tributaries that dominate that part of the basin shown in Figure 4, with most of the fishing activities taking place in the Keep River main channel located in the Northern Territory. Similarly, some subcatchments located in the upper reaches of the Fitzroy, Isdell and Lennard Rivers were identified as highly accessible. To our knowledge there are few large permanent waterholes (and probably low abundance of target species) in each of these areas. Whether this results in relatively low fishing pressure, or a concentration of fishing pressure in permanent waterholes, is unknown.

Management of freshwater fisheries has typically focused on the effects of commercial and recreational fishing in 'trophy' fisheries, e.g. the Murray cod in the Murray Darling Basin (Humphries & Winemiller 2009). Remote and intermittent rivers present significant challenges for natural resource managers, due to difficulties in implementing protective policies and legislation in remote areas (Datry *et al.* 2014) and because applicability and transferability of resource monitoring, stock assessment, and development of fisheries management regulations in rivers with intermittent flow, and where the predominant harvest is customary and recreational, is largely unknown.

Fisheries management regulations are driven by specific policy requirements and with an understanding of the nature of the fishery and the spatial and temporal scales of the resource. Monitoring programs or survey designs are therefore customised for specific management objectives (Hartill *et al.* 2012), which may be catch, biological, social or economic in nature. The EBFM approach currently implemented in the Kimberley region includes monitoring of indicator species (i.e. barramundi and silver cobbler) in the Ord and Fitzroy river basins and focuses on an assessment of compliance with regulations that govern the harvest of fish by Aboriginal or recreational fishers in Western Australia. The EBFM approach employed in Western Australia is ideally suited to include a variety of monitoring techniques to quantify the resource use and changes in the condition of ecosystem components, including for example, habitats and the abundance of targeted fish species. Extending current monitoring to include i) popular fishing areas in subcatchments of the Lennard and King Edward river basins and ii) additional information on actual fish harvest and the abundance of targeted fish species, will provide a better understanding the current fishing pressure and its impact on the fisheries resource, as well as confirmation of the proposed method's predictive capability for this region. Options for providing the additional data to inform management of fisheries across the region could include one-off surveys or long-term monitoring of target fish communities, using fisheries dependent and/or independent monitoring techniques, to provide information on either absolute (e.g. total catch) or relative (e.g. catch indices) estimates of fish harvest. Assessment of the distribution of fishing activities and the likely 'pressure' (e.g. number of fishers, number of fish caught) using either on-site and/or off-site surveys of fishers would also be beneficial. Sampling designs need to be at appropriate spatial and temporal scales, with appropriate replication to achieve required precision, to inform changes in harvest levels, decision-making and policy development.

Additional knowledge on 'site-choice' by both Aboriginal and recreational fishers could also contribute valuable information to the EBFM. While some data on the dynamics of Aboriginal use of permanent river pools exists from northern Australia (Jackson *et al.* 2012), similar information that indicates the use of these areas for recreational fishing is limited. Knowledge of the factors that determine 'site choice' by fishers utilising freshwater ecosystems is generally scarce, despite its importance to the development of effective management. Knowing why fishers fish where they do, for example, would refine the prediction of areas currently experiencing high fishing pressure, and those areas that may be subject to high fishing pressure in the future. Important criteria for site choice identified in previous studies include: cost (i.e. travel cost); fishing quality (e.g. size and abundance of target species); environmental quality (terrestrial aesthetics and water quality); facility development (boat ramps and accommodation); encounter levels (i.e. with other anglers), and; fishing regulations (e.g. site or seasonal closures) (see Hunt & Ditton 1997; Schramm *et al.* 2003; Hunt 2005). Nonetheless, in the context of the Kimberley, which is largely only accessible during the dry-season, accessibility may be expected to determine much of the spatial dynamics of fishing pressure (Close *et al.* 2014).

CONCLUSION

In an area as vast and difficult to access as the Kimberley region of Western Australia, knowledge of those areas that are easily accessed and therefore likely to experience higher fishing activity than more remote areas, should provide opportunities to prioritise areas for monitoring and management of the fisheries resource and other ecosystem assets. Using relationships between site accessibility and the abundance of large-bodied fish species developed from the Fitzroy River catchment, this Kimberley-wide assessment of potential fishing pressure identified that subcatchments in the Fitzroy, Lennard, King Edward and Ord river basins are likely to experience relatively high fishing activity. In the context of the Kimberley region, subcatchments may provide an appropriate spatial scale for management; within the basins listed above, subcatchments in the Lennard and King Edward river basins represent potential areas to which the ecosystem based fisheries management approach used in Western Australia could be extended. A variety of monitoring programs could be included in the EBFM approach at these sites to quantify, not only the use of aquatic resources by Aboriginal and recreational fishers, but also the condition of ecosystem assets such as the abundance of targeted species.

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Predator and prey interactions of fishes of a tropical Western Australia river revealed by dietary and stable isotope analyses

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Stomach content analyses of fishes occurring in the Fitzroy River, Western Australia, were used to investigate seasonal and ontogenetic changes in the diets and feeding relationships of the most abundant teleost and elasmobranch species. Concurrent analysis of $\delta^{13}C$ and $\delta^{15}N$ isotope ratios was also used to determine which food resources were energetically important to each species (assimilated) and included less common fishes for which few dietary samples were attained. The use of $\delta^{13}C$ and $\delta^{15}N$ isotope and stomach content analysis indicated that differences often exist between the food types consumed and those that are energetically important to a species. Dietary analysis suggested that aquatic insects, and to a lesser extent filamentous algae, were important food sources for many of the species present. While stable isotope analysis also suggested that insects are important prey, both insects and algae did not appear to be as important as direct energy sources. In contrast, prey types that persist throughout the year (e.g. fish, molluscs and *Macrobrachium spinipes*) may be more important sources of energy than dietary data revealed. For example, isotope analysis suggested that fish are an important energy source for a large number of species including several which have been considered to be strict algivores/detritivores. Dietary overlap between species was found to be the highest during the wet season, when prey availability was presumably also high, decreased in the early dry season as fishes became more specialised in their feeding and increased again in the late dry when food became very limited.

KEYWORDS: ontogeny, stomach content analysis, isotope analysis, food web

INTRODUCTION

Seasonality is recognised as a major factor affecting the diets and trophic relationships of riverine fishes via its effects on habitat availability, migration patterns, assemblage structure and prey availability (Zaret & Rand 1971; Angermeier and Karr 1983; Ross *et al.* 1985; Sumpton & Greenwood 1990; Winemiller & Jepson 1998). This influence is particularly relevant in highly seasonal systems such as tropical (monsoonal) rivers where the magnitude of flood events is important in determining their biological compositions (Bunn & Arthington 2002) and underpins river ecosystem function (Puckridge *et al.* 1998).

Fish communities of tropical Australian rivers are unique and have been shown to differ from those of Asia, Africa and South America (Unmack 2001; Allen *et al.* 2002). In the latter, terrestrially derived plant material and detritus are significant direct food sources for numerous species and these in turn support an abundant and diverse piscivorous fauna (Lowe-McConnell 1987). In contrast, dietary studies of fishes in tropical Australian rivers indicate that few species exclusively occupy the top and bottom trophic levels, with omnivorous species that consume a broad range of food types from multiple trophic levels being prevalent (see for example Arthington 1992; Pusey *et al.* 1995, 2000; Bishop *et al.* 2001; Morgan *et al.* 2004a; Davis *et al.* 2010). However, relatively few dietary studies of tropical Australian riverine fishes have investigated changes in diet over time, in response to seasonal variation or ontogenetic change. Despite some recent exceptions, including the study of Raynor *et al.* (2010) who investigated temporal food web dynamics and those of Davis *et al.* (2011, 2012, 2013) who investigated ontogenetic dietary changes in Australian Terapontids, the description of many Australian species as being 'generalists' or 'omnivorous' remains, which may be partly attributed to the limited understanding of how diets vary over time in those species. Seasonality, for example, is known to greatly influence the prey availability of tropical food webs and as such dietary overlap (Lowe-McConnell 1987; Prejs and Prejs 1987; Winemiller 1989). As discussed by Matthews (1988), increases in dietary overlap can occur when food becomes very limited, however, it can also occur as a result of an abundance of prey sources. In consideration of this, dietary studies based on a single sampling event or in one season for example, would not detect changes in the prey available or the utilisation of that prey by a particular species.

The analysis of a fish's diet through quantification of stomach contents provides a 'snapshot' of the food recently consumed (Pinnegar & Polunin 1999). To obtain an accurate depiction of the overall diet of a species utilising this method numerous samples are required and classification of a species feeding habit (e.g. as a detritivore, insectivore or piscivore) can only be ascertained when diets are inspected over time or at least seasonally (Jepson & Winemiller 2002). Difficulties also often exist when attempting to classify fishes with broad diets, those which feed at multiple trophic levels (i.e. omnivores) or those that feed opportunistically (Yoshioka & Wada 1994; Jepson & Winemiller 2002). These difficulties may be compounded by the reality that the presence of a food item in a stomach does not necessarily indicate that it is energetically important to that species (or assimilated) and that differences in digestion rates of different food types can lead to the over or under-representation of those prey types in the diet (Forsberg *et al.* 1993; Vander Zanden *et al.* 1997; Pinnegar & Polunin 1999; Melville & Connolly 2003).

In contrast to stomach content analyses, the stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios of a consumer can aid in the depiction of the organic source (primary producer of the system) and trophic position of the consumer, respectively, by determining those foods actually assimilated into tissues (DeNiro & Epstein 1981; Fry & Sherr 1984; Peterson & Fry 1987; Yoshioka & Wada 1994; Post 2002). Thus, in cases where dietary analysis reveals a broad range of food types, stable isotope analysis may be employed to investigate the assimilation of ingested food items, assist in the clarification of trophic interactions occurring between consumers, and trace variations of a species diet in response to, for example, seasonal food abundances and ontogenetic changes (Bunn & Boon 1993; Cocheret de la Morinière *et al.* 2003).

The paucity of detailed information on the dietary interactions of tropical freshwater fish communities in Australia and the inapplicability of foreign studies to a region that has a highly endemic ichthyofauna (Allen *et al.* 2002) generated this study's aims. These were to describe and compare the seasonal diets and feeding relationships of the different size classes of the most abundant teleost and elasmobranch species found in freshwaters of a large tropical river system of northern Australia using both stomach content and stable isotope analyses. The use of both techniques allowed dietary changes of fishes captured in low abundance (including *Pristis pristis* which is protected in Australia under the *Environment Protection and Biodiversity Conservation Act 1999*) to be investigated and also provided the basis for comparing the effectiveness of each technique in identifying the most important prey to the fish species present. These data were also used to investigate whether herbivores/detritivores and piscivores are under-represented in tropical Australian systems and provide a basis for comparisons to the criteria described by Lowe-McConnell (1987) for tropical systems of Asia, Africa and South America. Following Matthews (1998), we subsequently test the hypotheses that there is likely to be higher magnitudes of dietary overlap between species when prey availability is high (in this case the monsoonal wet season), that it will become reduced in the early dry season as resources begin to contract and the diets of each species becomes more specialised, and will increase when resources become very limited (in the late dry season).

MATERIALS AND METHODS

Sampling locality, seasonality and methods of collection

The Fitzroy River is one of the largest unregulated rivers in northern Australia, draining almost 90 000 km², and receives ~90% of its annual rainfall during the wet season (between November and March) (Anon 1993; Ruprecht & Rogers 1998). Fish were collected from the Fitzroy River in June 2003, November 2003 and March 2004 to coincide with the early dry, late dry and wet seasons, respectively. In light of the high flow rates and flooding that occurs in the Fitzroy River during the monsoonal wet season (which preclude access to a vast majority of the system) sampling for freshwater fish was primarily conducted ~300 km from the mouth in the main channel at Geikie Gorge (between 18.110°S, 125.699°E and 18.013°S, 125.764°E). Geikie Gorge is a large permanent pool with extensive sandy shallows and backwaters. Flow rates are low or non-existent except during the peak wet season. Due to only low numbers of freshwater sawfish *Pristis pristis* and the bull shark *Carcharhinus leucas* being encountered in Geikie Gorge during the study some additional samples were collected from freshwater pools ~150 km downstream below Camballin Barrage (18.187°S, 124.492°E). This site is the next location downstream of Geikie Gorge that has road access, holds a comparable suite of fishes (see Morgan *et al.* 2004b) and was considered to have comparable densities and types of detritus, aquatic vegetation and large woody debris.

Opportunistic sampling of 18 teleost and two elasmobranch species was conducted during daylight hours using a combination of gill, seine and throw nets, and baited lines. In each season, efforts were made to collect at least 30 individuals (containing food in their stomachs) of each species that were representative of the size distribution present.

Dietary samples of *P. pristis* were obtained from a number of individuals that had been found dead or from those donated by indigenous fishers prior to consumption. Muscle tissue was also collected from these individuals for stable isotope analysis. Fin clips were also obtained for stable isotope analysis from captured individuals (prior to their release) with a total of nine tissue samples per season being collected. Zero, six and two dietary samples were obtained in the wet, early dry and late dry seasons, respectively.

Muscle tissue from nine, 13 and nine *C. leucas* was collected for stable isotope analysis in the wet, early dry and late dry seasons, respectively. Zero, 14 and 5 dietary samples were subsequently also obtained from these individuals.

Stomach contents – identification and quantification

The stomach was removed from each fish, its contents were examined and each food item identified to the lowest possible taxon. The percentage contribution of each item to the total stomach content was estimated and allocated to one of 41 prey categories (Tables 1–4) based on their similar size, position occupied in the water column and mobility (subsequently referred to as dietary categories) (Gill & Morgan 1998, 2003). Broad dietary categories were also determined from these for ease of interpretation (see Table 5).

Diets were analysed using the points method which gives the relative contribution of each prey type to the volume (percentage contribution (%V)) of stomach content of the fish (Hynes 1950; Ball 1961). The mean

Table 1 Average wet season diet (adjusted %V) of each fish species captured in freshwaters of the Fitzroy River. N.B. Cle - *Carcharhinus leucas*; Pp - *Pristis pristis*; Ne - *Nematalosa erebi*; Ng - *Neoarius graeffei*; Ma - *Melanotaenia australis*; Cl - *Cratocephalus lentiginosus*; Am - *Ambassis* sp. 1; Lc - *Lates calcarifer*; Ap - *Amniataba percoides*; Hj - *Hephaestus jenkinsi*; Lu - *Leiopotherapon unicolor*; Ga - *Glossamia aprion*; Tk - *Toxotes kimberleyensis*; and Gg - *Glossogobius giuris*.

Species and size category	*Ne<100*	*Ne>100*	*Ng<150*	*Ng >150*	*Ma*	*Cl*	*Am*	*Lc*	*Ap >40*	*Hj*	*Lu*	*Ga*	*Tk<50*	*Tk>50*	*Gg<70*	*Gg>70*
Length range (mm) min	57	151	110	216	26	23	11	487	51	120	33	44	19	59	23	74
max	87	332	130	391	55	38	53	951	83	362	107	180	49	91	67	155
n used in analysis	11	22	7	29	28	29	25	34	36	30	30	23	14	14	26	8
Dietary component																
Sand	0.45															
Diatom																
Filamentous algae	1.64	9.23	34.42	3.52					53.44	30.98	23.44					7.50
Fig/fruit		0.36		18.90				2.94		29.29						
Aquatic macrophyte										3.33						
Terrestrial vegetation		3.41	4.96	11.56				4.12		20.52				0.55		
Biofilm/silt	97.73	86.05										3.11				
Gastropoda			2.30	0.34				0.29	0.56	0.08						
Bivalvia		0.09		0.13						0.08						
Nematoda		0.09														
Annelida				0.17												0.38
Terrestrial Arachnida				0.34	4.29									10.61		
Aquatic Arachnida																
Ostracoda	0.18		3.30		0.89	14.38	1.00		1.71		0.17				47.97	
Cladocera		0.09				6.87	13.13		0.35							
Copepoda						1.21			0.14		0.33				0.77	1.25
Isopoda											1.00					
Amphipoda							4.00		0.14			0.87				
Shrimp (<15mm)				0.14												
Macrobrachium spinipes				9.36				40.29								
Diptera larvae			7.97		5.09	10.28	23.03		6.25		6.06	0.87	7.92		3.88	
Diptera pupae					4.61	30.86	28.63		0.14		2.12	0.87	18.42		20.95	
Aquatic Hemiptera		0.68	12.14		13.27	27.09	15.47		8.51		20.83	70.40	27.41	18.06	13.54	43.75
Trichoptera larvae			1.43		0.18				0.92		0.64			3.83	0.77	
Odonata larvae					1.79		1.20		1.60		2.24			3.57	2.69	
Ephemeroptera larvae					3.99	3.10	9.33		1.67		0.20	1.74				
Coleoptera larvae			5.49				0.60		10.28		1.00	1.30	13.93		7.50	
Aquatic Coleoptera adult			14.64	0.25	21.65				7.92		15.54	5.37	13.77	4.37	1.92	12.50
Diptera adult				0.17	3.04						1.50		0.75	1.90		
Ephemeroptera adult									0.28							
Lepidoptera adult				0.34										6.88		
Orthoptera adult			8.57	29.83				5.88		11.71	9.00		10.56	16.25		11.25
Odonata adult				0.34												
Terrestrial Coleoptera adult				18.77	3.21					0.67		2.17		15.46		
Hymenoptera (flying) adult					3.57								4.40	7.22		
Hymenoptera (non-flying) adult				0.28	34.42						2.22	1.09	2.84	11.31		
Teleost				2.07		3.45		46.47	6.11	3.33	10.33	12.20				23.38
Teleost Scales			4.76	3.46							3.38					
Teleost Egg						2.76	3.60									
Mammal																
Reptile																

Table 2 Average early dry season diet (adjusted %V) of each fish species captured in freshwaters of the Fitzroy River. See Table 1 for species codes.

Species and size category	*Cle*	*Pp*	*Ne<100*	*Ne >100*	*Ng<150*	*Ng>150*	*Ma*	*Cl*	*Am*	*Lc*	*Ap<40*	*Ap>70*	*Hj*	*Lu*	*Ga*	*Tk >50*	*Gg*
Length range (mm) min	778	912	25	138	92	207	41	16	19	434	17	72	137	40	20	50	13
max	1160	2271	56	340	132	380	54	48	46	928	37	87	325	108	120	193	48
n used for analysis	14	6	19	36	18	30	31	31	24	30	26	4	25	28	28	19	29
Dietary component																	
Sand		3.62		2.52	4.21	4.29				0.17		1.96	1.23				
Diatom				0.64													
Filamentous algae		13.89		24.18	6.02	5.11	23.23	0.86	4.17		0.58	45.39	70.88	18.63	2.42		
Fig/fruit					1.11	0.39	1.02						5.24	2.86			
Aquatic macrophyte	0.36					0.95											
Terrestrial vegetation	0.79	2.69	12.15	4.45	2.76	5.56							2.09	2.20		0.35	
Biofilm/silt		2.59		67.56									0.21				
Gastropoda					5.68	0.42						24.51					
Bivalvia				0.03	3.41												
Nematoda		0.33							4.79								
Annelida				0.34	2.83								0.44	2.50			
Terrestrial Arachnida							1.52										
Aquatic Arachnida							0.65										
Ostracoda								1.29	0.42					1.07	0.54		
Cladocera			47.31	0.27			14.92	4.43				21.88	0.22				2.07
Copepoda			40.43								1.65						
Isopoda											1.54						4.14
Amphipoda																	
Shrimp (<15mm)																	
Macrobrachium spinipes	0.71	10.24				3.98	0.85			20.83			9.60		3.57	0.53	
Diptera larvae					4.83	2.76	1.16	75.00	9.58		14.32	1.58	0.22	6.82	6.93		8.28
Diptera pupae									31.88		0.77	1.56			0.18	0.26	
Aquatic Hemiptera			0.11		28.09	6.36	8.18	10.05	24.58		9.28	3.13	3.59	26.90	24.80	6.67	10.17
Trichoptera larvae					2.56	1.46		0.51	5.00		9.38		0.24	8.79	3.85		30.69
Odonata larvae						5.38					0.20			9.58	5.45		
Ephemeroptera larvae						1.23	7.63	7.85			61.14			3.73	4.82		41.38
Coleoptera larvae					3.51	0.26	2.22		7.08		1.15			9.12	18.75		
Aquatic Coleoptera adult	7.14				18.84	1.38	7.22		12.50				2.19	1.70	15.79	17.50	
Diptera adult						0.54	5.32									2.51	
Ephemeroptera adult							0.76										
Lepidoptera adult						1.00											
Orthoptera adult					2.22	35.47	0.32								1.65	13.92	
Odonata adult						1.04										0.53	
Terrestrial Coleoptera adult					6.03	15.81	1.43						3.62			27.58	
Hymenoptera (flying) adult						2.22	0.65									11.96	
Hymenoptera (non-flying) adult								20.83								1.79	18.19
Teleost	83.14	66.63			5.68	2.86				79.00					9.46		3.28
Teleost Scales					2.22	1.54							0.22				
Teleost Egg							2.11							6.10			
Mammal	7.86																
Reptile																	

Table 3 Average late dry season diet (adjusted %V) of each fish species captured in freshwaters of the Fitzroy River. See Table 1 for species codes.

Species and size category	*Cle*	*Pp*	*Ne>100*	*Ng>150*	*Ma*	*Cl*	*Am*	*Lc*	*Ap40-70*	*Ap>70*	*Hj*	*Lu*	*Ga*	*Tk<50*	*Tk>50*	*Gg<70*
Length range (mm) min	878	1040	143	167	27	20	18	360	45	72	81	31	19	15	85	19
max	1328	1587	420	455	74	55	63	770	67	109	262	112	117	42	219	66
n used in analysis	5	2	44	33	30	30	21	30	19	10	22	17	31	18	12	29
Dietary component																
Sand		5.49	26.36	1.49												
Diatom																
Filamentous algae			21.42	8.20	56.69	18.92			18.85	16.66	51.85	1.38				0.69
Fig/fruit			0.34	8.48							25.77					
Aquatic macrophyte					0.42								2.30			
Terrestrial vegetation		2.75	2.09	2.26							11.20					
Biofilm/silt		66.37	48.67													
Gastropoda				4.98						2.43						0.86
Bivalvia		1.65	0.05	1.62							0.33		0.18			
Nematoda						0.17										1.38
Annelida			0.05													
Terrestrial Arachnida														3.89		
Aquatic Arachnida					0.21		32.43									
Ostracoda				0.15	0.04	44.05	18.41		3.12	28.17		1.27	6.45			27.07
Cladocera			0.11			2.39				0.20			3.39			
Copepoda			0.27													
Isopoda							0.73			0.10						
Amphipoda			0.05													
Shrimp (<15mm)																
Macrobrachium spinipes		2.75		0.84				19.33			0.27		3.23			
Diptera larvae			0.05	0.36	0.13	3.75	5.58		13.25	3.02	0.33	10.75	7.85	15.33	0.42	9.58
Diptera pupae					2.33	13.72						13.21	4.52	33.19		2.11
Aquatic Hemiptera				2.17	8.62	6.03	19.94		7.98		0.99	15.23	18.72	31.09	8.43	27.61
Trichoptera larvae			0.32	0.24	0.17	7.19	8.40		2.98	1.68		10.55		1.31		3.83
Odonata larvae				5.45					10.53	39.42	1.84	20.59	7.67	2.61		
Ephemeroptera larvae									15.79			0.29				1.15
Coleoptera larvae					0.67	3.79	10.06		24.47			8.09	3.23			14.79
Aquatic Coleoptera adult				4.55	2.24		1.12				1.15	6.86	6.45	2.53	18.95	2.93
Diptera adult					3.29		3.33				0.25	0.88	1.61			
Ephemeroptera adult				1.82												
Lepidoptera adult															7.50	
Orthoptera adult				23.43											19.57	
Odonata adult				2.70					2.37		0.25	5.00		0.69	3.33	
Terrestrial Coleoptera adult				10.05	0.07									3.40	19.40	
Hymenoptera (flying) adult				3.03						8.33					0.83	
Hymenoptera (non-flying) adult					0.40	25.15									5.96	21.57
Teleost	80.00	20.99		6.36				80.67			5.50	5.88	29.03			8.00
Teleost Scales			0.23	7.19					0.66		0.25					
Teleost Egg													2.15			
Mammal				1.21												
Reptile	20.00			3.00									3.23			

Table 4 Percentage contribution (%V) of food items found in the stomachs of fishes captured in low abundance or in only one season from freshwaters of the Fitzroy River.

Species	*Elops hawaiensis*	*Megalops cyprinoides*	*Neosilurus hyrtlii*	*Strongylura krefftii*	*Hannia greenwayi*	*Liza alata*
n	3	16	13	9	3	21
Dietary component						
Sand			0.48			22.03
Diatom						15.30
Filamentous algae	11.43		3.71	3.10	65.00	17.89
Fig/fruit						
Aquatic macrophyte						
Terrestrial vegetation			0.55			0.48
Biofilm/silt	28.57		6.25			43.47
Gastropoda			16.71			
Bivalvia		1.42	1.92			
Nematoda						0.06
Annelida			0.41			
Terrestrial Arachnid						
Aquatic Arachnid						
Ostracoda			64.01			
Cladocera			0.40			
Copepoda						
Isopoda						
Amphipoda						
Other microcrustacea						
Shrimp (<15mm)						
Macrobrachium spinipes						
Diptera larvae			1.84			
Diptera pupae						
Aquatic Hemiptera	38.57	37.74	0.55	13.33	10.00	
Trichoptera larvae			0.10			
Odonatan larvae		2.26		1.67		
Ephemeroptera larvae						
Coleoptera larvae						
Aquatic Coleoptera adult		24.53		5.71		
Diptera adult		1.32				
Ephemeroptera adult						
Lepidoptera adult						
Orthoptera adult		1.89				
Odonata adult		1.70				
Terrestrial Coleoptera adult		2.36				
Hymenoptera (flying) adult						
Hymenoptera (non-flying)						
Other terrestrial insect						
Unidentified insect part	21.43	13.21	3.08	8.81		
Neoarius graeffei						
Glossamia aprion						
Nematalosa erebi				27.14		
Amniataba percoides						
Craterocephalus lentiginosus		3.40		11.90	25.00	
Other/unidentified teleost		10.19		23.33		
Teleost scales						
Teleost egg						
Mammal						
Reptile				5.00		

percentage volumetric contribution (%V) of each of the reassigned dietary categories to the stomach contents of each of the fish species was calculated for each season.

Stomach contents – differences between size categories and seasons within a species

To investigate both ontogenetic and temporal changes in diet, the total lengths (mm) recorded for individuals within each species were examined and three respective size categories (groupings) were assigned based on length frequency analyses. Size categories (mm) identified for the 12 most abundant teleost species (i.e. those for which sufficient numbers for analysis were collected in all seasons) were as follows: *Nematalosa erebi* <100, 100–250, >250; *Neoarius graeffei* <150, 150–250, >250; *Melanotaenia australis* <40, 40–50, >50; *Cratocephalus*

Table 5 Summary of stomach contents (%V) of fishes in the Fitzroy River during the wet, early dry and late dry seasons. *(Cle, C. leucas; Pp, P. pristis; Ne, N. erebi, 1<100mm, 2>100mm; Ng, N. graeffei, 1<150mm, 2>150mm; Ma, M. australis; Cl, C. lentiginosus; Am, Ambassis sp 1; Lc, L. calcarifer; Ap, A. percoides, 1<40mm, 2>40mm<70mm, 3>70mm; Hj, H. jenkinsi; Lu, L. unicolor; Ga, G. aprion; Tk, T. kimberleyensis, 1<50mm, 2>50mm; Gg, G. giuris, 1<70mm, 2>70mm).*

Species and size	*Cle*	*Pp*	*Ne1*	*Ne2*	*Ng1*	*Ng 2*	*Ma*	*Cl*	*Am*	*Lc*	*Ap1*	*Ap2*	*Ap3*	*Hj*	*Lu*	*Ga*	*Tk1*	*Tk2*	*Gg1*	*Gg2*
Wet season *n*	0	0	11	22	7	29	28	29	25	34	0	36	0	30	30	23	14	14	26	8
Biofilm/silt/sand			98	86												3				
Vegetation			2	13	40	34				8		53		84	23			<1		8
Aquatic vegetation			2	9	35	4						53		34	23					8
Terrestrial vegetation				4	5	30				8				50				<1		
Aquatic Invertebrata			<1	1	47	10	51	94	96	40		40			40	81	81	30	100	58
Aquatic worms				<1		<1								<1						<1
Aquatic Mollusca				<1	2	<1				<1		<1		<1						
Aquatic Arthropoda				<1	45	10	51	94	96	40		40			40	81	81	30	100	58
Terr. Invertebrata					9	50	49			6		<1		12	13	3	19	70		11
Teleostei					5	6		6	4	46		6		3	14	12				23
Mammalia/ Reptilia																				
Early dry season *n*	14	6	19	36	18	30	31	31	24	30	26	0	4	25	28	28	0	19	29	0
Biofilm/silt/sand		6		70	4	4				<1			2	1						
Vegetation	1	17	12	29	10	12	24	1	4		<1		45	78	24	2		<1		
Aquatic vegetation	<1	14		25	6	6	23	1	4		<1		45	71	19	2				
Terrestrial vegetation	1	3	12	4	4	6	1							7	5			<1		
Aquatic Invertebrata	8	11	88	1	70	23	43	99	96	21	99		53	14	63	85		25	97	
Aquatic worms		<1		<1	3				5					<1	2					
Aquatic Mollusca				<1	9	<1	1						25							
Aquatic Arthropoda	8	10	88	<1	58	23	42	99	91	21	99		28	14	61	85		25	97	
Terr. Invertebrata					9	56	31							4		3		75		
Teleostei	83	67			8	4	2			79				<1	6	9			3	
Mammalia/ Reptilia	8																			
Late dry season n	5	2	0	44	0	33	30	30	21	30	0	19	10	22	17	31	18	12	29	
Biofilm/silt/sand		72		75		1														
Vegetation		3		24		19	57	19				19	17	89	1	2			<1	
Aquatic vegetation				21		8	57	19				19	17	52	1	2			<1	
Terrestrial vegetation		3		2		11								37						
Aquatic Invertebrata		4		1		20	14	82	97	19		78	75	5	87	62	86	28	92	
Aquatic worms				<1				<1											1	
Aquatic Mollusca		2		<1		7							2	<1		<1			<1	
Aquatic Arthropoda		3		1		14	14	82	97	19		78	73	5	87	61	86	28	89	
Terr. Invertebrata						41	28		3			2	8	<1	6	2	14	72		
Teleostei	80	21		<1		15				81		<1		6	6	31			8	
Mammalia/Reptilia	20					4										3				

lentiginosus <30, 30–40, >40; *Ambassis* sp. 1 <25, 25–40, >40 (*sensu Ambassis* sp. 1 in Morgan *et al.* (2004) and *Ambassis* sp. in Allen *et al.* 2002); *Lates calcarifer* <550, 550–750, >750; *Amniataba percoides* <40, 40–70, >70; *Hephaestus jenkinsi* <150, 150–225, >225; *Leiopotherapon unicolor* <55, 55–85, >85; *Glossamia aprion* <40, 40–80, >80; *Toxotes kimberleyensis* <50, 50–110, >110; *Glossogobius giuris* <30, 30–70, >70. Dietary data for all individuals of the six respective species collected in only low numbers or in one season were combined.

To compare dietary differences between size classes within each species, the volumetric data of each individual was used. Dietary categories that were unidentifiable were excluded as their inclusion has the potential to bias multivariate analysis (Pusey *et al.* 2000). All other values were subsequently adjusted upwards to sum 100%. This adjustment is based on the assumption that the removed unidentified fractions consist of the same proportions as the identified food items present in the stomach (Pusey *et al.* 2000).

The adjusted dietary data for individuals within each size category of each species within a season were then used to construct a similarity matrix using the Bray-Curtis similarity coefficient with PRIMER 5.1.2 (Clarke and Gorley 2001). A one-way analysis of similarity (ANOSIM) was subsequently used to determine if dietary differences between size categories were significant, and the R-stat values produced used to indicate the magnitude of these differences. Examination of R-statistics revealed that in no cases did values of 0.3 or less have p-values approaching anywhere near 0.05. Thus R-statistics of less than 0.3 were not considered to be significant. Size categories were combined if there was no significant difference. As only low numbers of *C. leucas* and *P. pristis* were collected, diet data for all individuals were combined for each season.

Stomach contents – comparisons between species within a season

Dietary data for individuals of each species within each reassigned size category were compared using a similar approach, i.e. using the data from the individual stomach and ANOSIM, to test the hypothesis that dietary overlap will be higher in the wet and late dry seasons than in the early dry season. As no *C. leucas* or *P. pristis* dietary samples were collected in the wet season these species were not included when calculating the percentage of non-significant results in the early dry season and late dry season. The overall mean diet of each species (and size category within) was subsequently calculated and used to generate dendograms to illustrate the feeding groups present.

In addition to the 20 species/size categories used in the above analyses giant herring *Elops hawaiensis*, oxeye herring *Megalops cyprinoides*, Hyrtl's tandan *Neosilurus hyrtlii*, freshwater longtom *Strongylura krefftii*, Greenway's grunter *Hannia greenwayi* and giant gudgeon *Oxyeleotris selheimi* were also caught during this study. As these species were caught in low numbers, in only one or two seasons and often had little or nothing in their stomachs, they were not used in the above analyses. When available their diets are reported and their flesh was used in the stable isotope analyses.

Stable isotope analyses – sample collection

In general, individual fish used for stable isotope analysis were the same as those upon which stomach content analysis was conducted. Fifteen individuals from each teleost species (and size category within a species identified by dietary analysis) and other food web components were analysed in each season. Nine samples were used for analysis of *P. pristis* and *C. leucas* in each season. In the case of *P. pristis*, an endangered species, analysis was based on either fin clips taken prior to their live release or muscle tissue attained from the few individuals from which the stomach was removed. Fin tissue has been shown to be a close predictor of muscle tissue values (see for example Kelly *et al.* 2006; Jardine *et al.* 2011) and was considered appropriate for investigating the trophic position of this rare species.

Cherabin (*Macrobrachium spinipes*), two gastropod molluscs (a small snail (Pomatiopsidae) and large snail (Hydrobiidae)) and two bivalve molluscs (a freshwater mussel (Hyriidae) and pea clam (Sphraeriidae)) were collected. The deposition of a thick layer of silt precluded the collection of the last of these species in the wet season. Terrestrial Orthoptera (grasshoppers; Acrididae) and aquatic hemipterans (water strider; Gerridae) were also collected. These latter taxa were amongst the only terrestrial and aquatic insects that could be readily collected in sufficient numbers to provide enough tissue for analysis.

Leaves from the most conspicuous riparian plant species in Geikie Gorge (and common throughout the Fitzroy River catchment), i.e. grasses, pandanus *Pandanus aquaticus*, river gum *Eucalyptus camaldulensis*, silver cadjeput *Melaleuca argentea* and the freshwater mangrove *Barringtonia acutangula* were collected by hand from the living plant. Filamentous algae was also collected by hand but could not be gathered in the wet season due to silt deposition. A seasonally abundant aquatic reed was also collected by hand during the late dry season. Three, 5 cm sediment cores were also collected in each season. All samples were placed into individual bags and placed on ice until they could be frozen.

Stable isotope analyses – sample preparation

All animal and plant samples were rinsed in distilled water. White muscle, which is less variable in $\delta^{13}C$ and $\delta^{15}N$ than other tissues (Tieszen *et al.* 1983; Pinnegar & Poulin 1999), was carefully removed from fishes, eliminating as much bone, skin and red muscle as possible. Skin and cartilage were excluded from fin clips of *P. pristis*. Equal quantities of muscle tissue from between nine and 15 randomly selected individual fishes of each species (and size) were evenly divided into three replicates for each season. Where fewer than nine individuals were collected per species, muscle samples were combined and divided into three pseudo-replicates (as per Beatty *et al.* 2005).

Abdominal tissue (carapace and intestine removed) was removed from 15 *M. spinipes* per season and randomly assigned to three replicates. Muscle tissue from between 10 and 20 individuals (depending on size) of each mollusc was removed and randomly assigned to one of the three replicates within each season collected. Muscle tissue was also obtained from the hind legs of approximately 20 orthopterans in the wet season. This quantity, however, was only sufficient for a single sample. At least 30 aquatic hemipterans were included in each replicate and macerated. Muscle tissue from all invertebrates was placed in 1 M HCl for 24 hours (for 48 hours in the case of whole aquatic hemipterans) to remove inorganic carbonates and thoroughly rinsed with distilled water prior to drying.

Leaf samples of each terrestrial vegetation type collected in each season were divided into three replicates and the woody petiole removed from the leaf to aid in drying and grinding. Three replicates (of five individual samples each) of both benthic algae and an aquatic reed (for each season present) were also assembled. Each of the three sediment core samples collected in each season were rinsed several times through a 150 μm sieve in order to collect organic detrital samples. Large detrital material was collected from the sieve and rinsed several times to provide samples of coarse particulate organic matter (CPOM). The fine material that passed through the sieve was washed and decanted several times with distilled water and collected to provide samples of fine particulate organic matter (FPOM). All samples were dried at 60 °C for 48 hours, and subsequently ground to a fine powder with a mortar and pestle.

Stable isotope analyses – analysis of $\delta^{13}C$ and $\delta^{15}N$

Between 2 and 2.5 mg of each animal tissue, 3 to 6 mg of each plant tissue and 20 to 50 mg of each particulate organic matter sample were placed in a capsule, combusted and analysed (one in 20 samples being analysed in duplicate) using a Tracermass Iron Ratio Mass Spectrometer (*Europa PDZ*, UK) fitted with a *Roboprep* combustion system to oxidize the samples. The ratios of 13C:12C and 15N:14N were subsequently presented as the relative part per thousand (‰) differences between the signatures of the sample and that of the international standards of Pee Dee Belemite for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$. The precision of the analytical equipment was ±0.1‰ for $\delta^{13}C$ and ±0.3‰ for $\delta^{15}N$. The means of each sample category are presented ± 0.01 s.e.

Stable isotope analyses – trophic position

To reflect trophic position, the mean $\delta^{15}N$ and $\delta^{13}C$ (‰) ratio of each sample was plotted in each season. Based on dietary analysis and dietary literature (see for example Bishop *et al.* 2001; Allen *et al.* 2002) each fish species was categorised as being either a piscivore, aquatic or terrestrial insectivore or detritivore/algivore and assigned a corresponding code (see Figures 4, 5 and 6). As terrestrial and aquatic invertebrates were only able to be collected in a single season, their $\delta^{13}C$ and $\delta^{15}N$ signatures were also used in food web analyses in other seasons. In the case of the pea clam, which was deeply buried in silt during the wet season, values were not included in analyses as it was considered to be unavailable to fish.

The relative trophic position of each fish species to base level primary producers and potential food types were also estimated using the following formula (Post 2002):

$$TL_{sc} = 1 + (\delta^{15}N_{sc} - \delta^{15}N_{base}) / \Delta_n$$

where TL_{sc} is the trophic level of the consumer, $\delta^{15}N_{sc}$ is the mean stable nitrogen ratio (‰), $\delta^{15}N_{base}$ is the mean stable nitrogen ratio (‰) of the base of the food web (i.e. the overall mean $\delta^{15}N$ signature of the primary producers (aquatic and terrestrial) collected in each season, respectively), and Δ_n is the mean enrichment (‰) between trophic levels. During this study, a mean enrichment of 2.54 ‰ was used, in accordance with the meta-analysis of 134 estimates by Vanderklift & Ponsard (2003).

Stable isotope analyses – IsoSource mixing model

The isotopic signature of a consumer is rarely dependent upon the consumption of a single food source, but rather is a mixture and dependent upon the proportionate contributions of each food type (Fry & Sherr 1984). *IsoSource* (Phillips & Gregg 2003) was subsequently employed to investigate all the possible combinations of contributing sources of the mixture, by examining its proportions in small increments summed to 100%. Potential food sources used during analysis by *IsoSource* were those identified during stomach content analysis. Species relevant dietary literature (e.g. Bishop *et al.* 2001 and Allen *et al.* 2002) was also considered and any additional major prey item (i.e. not identified during our analyses of stomach contents) that was present in the Fitzroy River was included in the analysis. Dietary literature was particularly important for identifying potential food sources for those fish species encountered in only low abundance and those where stomachs were empty. In light of the relatively large number of potential food sources for each of the fishes analysed incremental increases of 2.5% were used to avoid impractical levels of computation. Although this is a relatively large value, Phillips & Gregg (2003) consider that it will provide an acceptable level of precision in determining the ranges of source contribution. The mass balance tolerance was also adjusted upwards from 0.5 ‰ (in increments of 0.1 ‰) until a feasible solution was achieved. While this upward adjustment reduces the precision of the computation and increases the range of the distributions, it does not alter the medians in feasible distributions (Phillips & Gregg 2003).

Six aquatic and terrestrial invertebrate food sources were collected during the current study. Although a wide range of invertebrate taxa are present and were encountered in the stomachs of fishes, the six taxa included in analysis were amongst the only invertebrate taxa that could be readily collected in sufficient abundance to provide enough tissue for analysis. While the signature of theses taxa may not typify those of all aquatic and terrestrial invertebrates, these six taxa were considered to be suitable proxies for aquatic and terrestrial invertebrate food sources as all were encountered during stomach content analysis and in some cases were the most abundant taxa of their respective broader food type categories. It should be noted that the inclusion of the limited number of invertebrates during *IsoSource* analysis may lead to the overestimation of the alternative food sources included in the analysis.

RESULTS

Trophic relationships of the fishes of the Fitzroy River

Dietary and isotope analyses were generally in accordance with regard to demonstrating that the majority of species have broad diets and are reliant on aquatic and/or terrestrial invertebrates (Tables 1–7, Figures 1–3). For example, dietary analyses indicated that the majority of species are feeding on a wide range of aquatic and terrestrial invertebrates with many also ingesting plant material and/or fishes. Estimation of trophic level using stable isotopes (Table 6, Figures 4–6) indicated that in all seasons fishes were more enriched in $\delta^{15}N$ than invertebrates, primary producers and detrital fractions. *IsoSource* modeling also confirmed the importance of invertebrates, plant material and fishes in those species in which they had been identified in the stomach contents (Table 7). Dietary data indicate that *C. leucas, P. pristis* and *L. calcarifer* are top order predators consuming fish, mammals and reptiles (*C. leucas*) or fish and large crustaceans (*P. pristis* and *L. calcarifer*) to the exclusion of almost all other dietary taxa. These species consistently occupied the highest trophic positions indicating their status as top order consumers and confirming their predominantly piscivorous diets. *Isosource* modeling confirmed this scenario. The two methods were not concordant with regards to the diets of *N. erebi* where stomach contents suggested that this species fed predominantly on biofilm/silt/sand and plant material, or in the case of smaller fish during the early dry season on aquatic arthropods (see Table 2). While

Table 6 Estimation of the trophic level (TL_{SC}) of consumer species collected from the Fitzroy River during the wet, early dry and late dry seasons.

	Wet Season Mean $\delta 15N_{base} = 4.94$		Early Dry Season Mean $\delta 15N_{base} = 4.42$		Late Dry Season Mean $\delta 15N_{base} = 3.05$	
Consumer	$\delta 15N_{SC}$	TL_{SC}	$\delta 15N_{SC}$	TL_{SC}	$\delta 15N_{SC}$	TL_{SC}
Elasmobranch						
C. leucas	13.09	4.21	13.19	4.45	12.48	4.71
P. pristis	11.46	3.56	12.66	4.24	12.51	4.73
Teleost						
N. erebi <100	10.47	3.18	11.28	3.70	–	–
N. erebi >100	8.55	2.42	7.88	2.36	8.84	3.28
E. hawaiensis	11.22	3.47	12.92	4.35	–	–
M. cyprinoides	11.46	3.56	–	–	12.69	4.79
N. graeffei <150	10.37	3.14	10.91	3.55	–	–
N. graeffei >150	–	–	11.28	3.70	11.23	4.22
A. dahli	9.82	2.92	–	–	–	–
N. hyrtlii	8.35	2.34	–	–	–	–
S. krefftii	–	–	13.21	4.46	10.83	4.06
M. australis	10.16	3.05	10.93	3.56	9.13	3.39
C. lentiginosus	10.43	3.16	10.45	3.37	8.53	3.16
Ambassis sp.1	10.42	3.16	10.56	3.42	8.45	3.13
L. calcarifer	11.17	3.45	11.76	3.89	11.97	4.51
A. percoides <40	–	–	10.19	3.27	9.69	3.61
A. percoides >40	10.04	3.01	10.95	3.57	10.90	4.09
H. greenwayi	–	–	11.20	3.67	–	–
H. jenkinsi	9.82	2.92	11.72	3.87	10.19	3.81
L. unicolor	10.71	3.27	10.65	3.45	9.17	3.41
G. aprion	9.68	2.87	11.17	3.65	8.63	3.20
T. kimberleyensis <50	10.46	3.17	–	–	8.53	3.16
T. kimberleyensis >50	10.37	3.14	10.97	3.58	10.78	4.04
O. selheimi	9.50	2.79	–	–	–	–
G. giuris <70	10.46	3.17	9.12	2.85	8.07	2.98
G. giuris >70	10.04	3.01	–	–	–	–
Crustacean						
M. spinipes (cherabin)	9.39	2.75	10.23	3.28	9.47	3.53
Mollusc						
(F) Hyriidae (mussel)	7.52	2.01	9.07	2.83	6.58	2.39
(F) Pomatiopsidae (sm snail)	6.08	1.45	6.09	1.66	6.98	2.54
(F) Hydrobiidae (lg snail)	6.85	1.75	5.86	1.57	7.00	2.55
(F) Sphaeriidae (pea clam)	–	–	8.47	2.59	6.68	2.43
Insect						
(F) Gerridae (water strider)	–	–	–	–	6.05	2.18
(F) Acrididae (grass hopper)	7.99	2.20	–	–	–	–

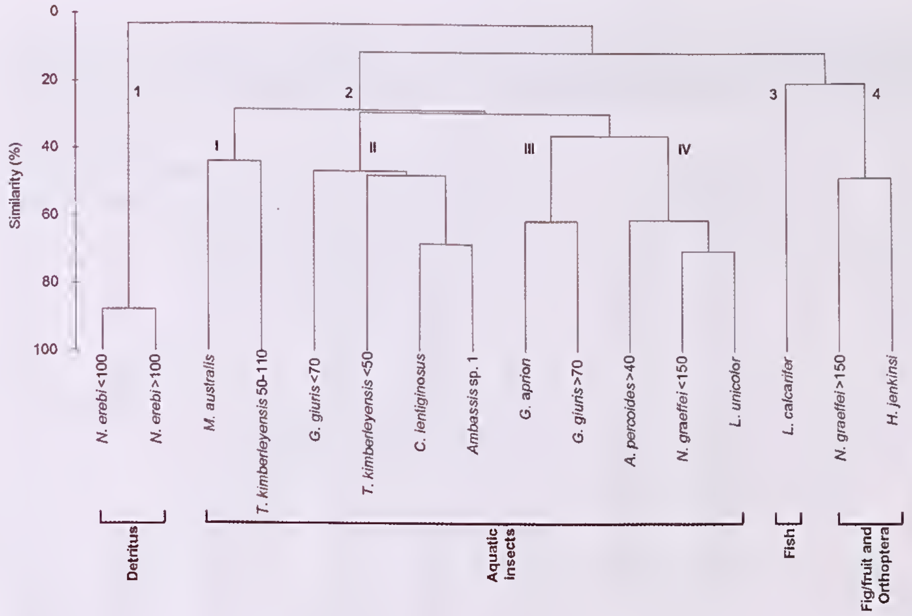

Figure 1 Classification of the mean volumetric dietary data of freshwater fishes of the Fitzroy River collected during the wet season, with major feeding groups indicated.

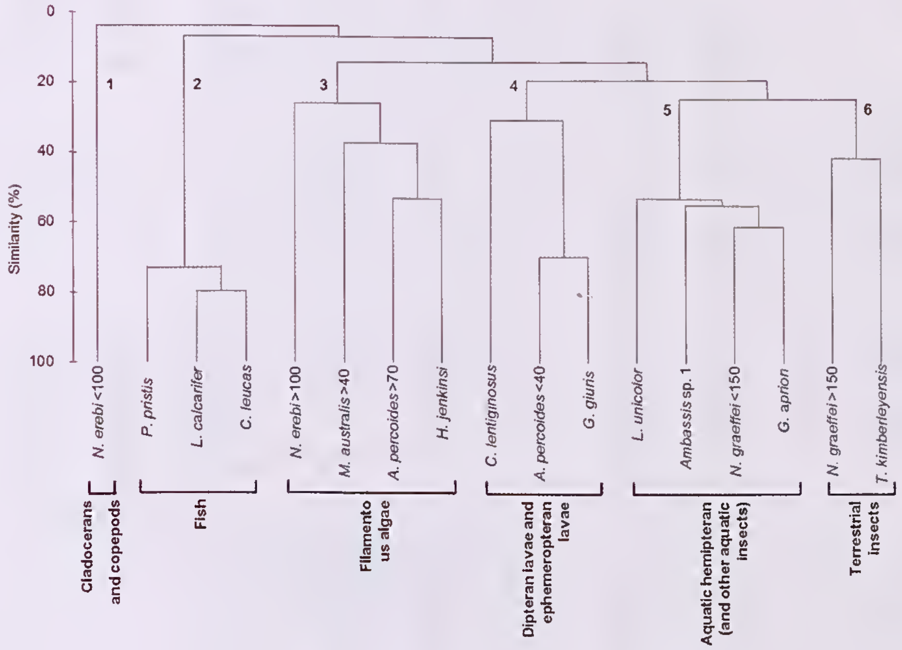

Figure 2 Classification of the mean volumetric dietary data of freshwater fishes of the Fitzroy River collected during the early dry season, with major feeding groups indicated.

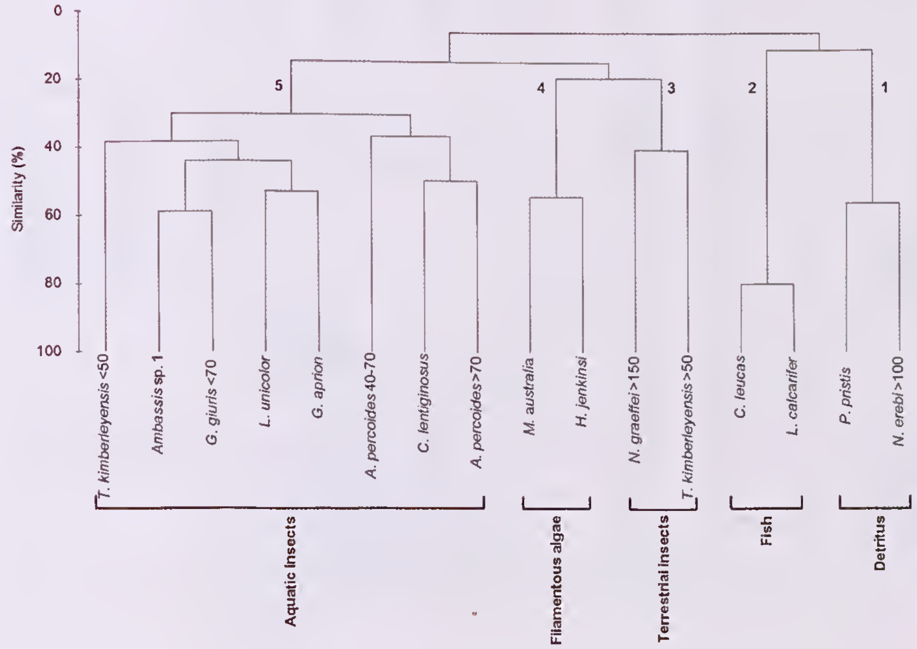

Figure 3 Classification of the mean volumetric dietary data of freshwater fishes of the Fitzroy River collected during the late dry season, with major feeding groups indicated.

Table 7 Feasible proportions (1st percentile, mean and 99th percentile) of food sources (determined by IsoSource) contributing to the diet of fish species (and sizes) captured in the Fitzroy River during the wet, early and late dry seasons. Potential food sources for each species were primarily determined from dietary analysis of fishes from the Fitzroy River.

		Wet season			Early dry season			Late dry season		
Consumer	Food sources	1st	mean	99th	1st	mean	99th	1st	mean	99th
C. leucas	*P. pristis*	0.60	0.78	0.95	0	0.96	1.00	0.25	0.72	0.98
	N. erebi <100	0	0.04	0.13	0	0	0	–	–	–
	N. erebi >100	0	0.02	0.08	0	0.01	0.03	0	0.01	0.03
	N. graeffei <150	0	0.12	0.30	0	0.01	0.03	–	–	–
	N. graeffei >150	–	–	–	0	0.03	0.10	0	0.26	0.73
	L. calcarifer	0	0.06	0.20	0	0.01	0.05	0	0.01	0.05
P. pristis	*N. erebi* <100	0	0.06	0.20	0	0	0	–	–	–
	N. erebi >100	0	0.03	0.13	0	0	0	0	0.02	0.08
	N. graeffei <150	0.43	0.68	0.88	0	0	0	–	–	–
	N. graeffei >150	–	–	–	0.93	0.94	0.95	0.90	0.95	1.00
	M. spinipes	0	0.10	0.40	0	0	0	0	0.03	0.10
	(F) Pomatiopsidae (sm snail)	0	0.3	0.13	0	0	0	0	0.01	0.05
	(F) Sphaeriidae (pea clam)	–	–	–	0	0	0	0	0.01	0.03
	Algae	–	–	–	0.05	0.06	0.08	0	0.00	0.03
	FPOM	0	0.01	0.08	0	0	0	0	0.00	0.03
	CPOM	0	0.02	0.08	0	0	0	0	0.00	0.03
N. erebi <100	(F) Pomatiopsidae (sm snail)	0	0.54	0.55	0	0.03	0.08	–	–	–
	(F) Sphaeriidae (pea clam)	–	–	–	0.93	0.93	0.95	–	–	–
	(F) Gerridae (water strider)	0	0.45	0.98	0	0.42	0.08	–	–	–
	Algae**	0	0.01	0.03	0	0	0	–	–	–
	M. argentea (silver cadjeput)	0	0.01	0.03	0	0	0	–	–	–
	FPOM	0	0.01	0.03	0	0	0	–	–	–
	CPOM	0	0.01	0.03	0	0	0	–	–	–
N. erebi >100	(F) Pomatiopsidae (sm snail)	0.80	0.89	0.96	0.03	0.64	0.98	0.88	0.95	1.00
	(F) Sphaeriidae (pea clam)	–	–	–	0	0.18	0.50	0	0.00	0.03
	Algae**	0	0.02	0.03	0	0.15	0.45	0	0.01	0.03
	M. argentea (silver cadjeput)	0	0.06	0.03	0	0.01	0.05	0	0.00	0.03
	FPOM	0	0.02	0.08	0	0.01	0.08	0	0.01	0.03
	CPOM	0	0.04	0.04	0	0.02	0.08	0	0.014	0.05
E. hawaiensis	*N. erebi* <100	0	0.01	0.05	0.03	0.46	0.70	–	–	–
	N. erebi >100	0	0.01	0.03	0	0.05	0.20	–	–	–
	C. lentiginosus	0	0.04	0.13	0	0.27	0.80	–	–	–
	(F) Gerridae (water strider)	0	0.02	0.08	0	0.02	0.10	–	–	–
	(F) Acrididae (grasshopper)	0.85	0.92	0.98	0.10	0.20	0.33	–	–	–
	Algae	–	–	–	0	0.01	0.08	–	–	–
	FPOM	0	0.02	0.05	0	0.01	0.05	–	–	–
M. cyprinoides	*N. erebi* <100	0	0.37	0.83	–	–	–	–	–	–
	N. erebi >100	0	0.06	0.20	–	–	–	0.55	0.78	0.95
	C. lentiginosus	0	0.27	0.78	–	–	–	0	0.10	0.10
	Ambassis sp.1	0	0.22	0.65	–	–	–	0	0.08	0.08
	(F) Hyriidae (mussel)	0	0.04	0.13	–	–	–	0	0.01	0.01
	(F) Sphaeriidae (pea clam)	–	–	–	–	–	–	0	0.01	0.01
	(F) Gerridae (water strider)	0	0.02	0.08	–	–	–	0	0.01	0.03
	(F) Acrididae (grasshopper)	0	0.03	0.15	–	–	–	0	0.03	0.04
N. graeffei <150	*N. erebi* <100	0	0.04	0.18	0.28	0.603	0.85	–	–	–
	C. lentiginosus	0	0.13	0.43	0	0.14	0.55	–	–	–
	G. giuris <70	0	0.17	0.53	0	0.10	0.43	–	–	–
	M. spinipes	0	0.13	0.48	0	0.03	0.15	–	–	–
	(F) Pomatiopsidae (sm snail)	0	0.03	0.13	0	0.05	0.02	–	–	–
	(F) Gerridae (water strider)	0	0.04	0.15	0	0.02	0.13	–	–	–
	(F) Acrididae (grasshopper)	0.25	0.45	0.70	0	0.02	0.08	–	–	–
	Algae	–	–	–	0	0.01	0.08	–	–	–
	CPOM	0	0.03	0.13	0	0.04	0.18	–	–	–

Consumer	Food sources	Wet season 1st	Wet season mean	Wet season 99th	Early dry season 1st	Early dry season mean	Early dry season 99th	Late dry season 1st	Late dry season mean	Late dry season 99th
N. graeffei >150	*N. erebi* <100	–	–	–	0	0.04	0.15	–	–	–
	C. lentiginosus	–	–	–	0	0.04	0.15	0	0.07	0.30
	G. giuris <70	–	–	–	0	0.02	0.10	0	0.04	0.18
	M. spinipes	–	–	–	0.10	0.34	0.53	0.08	0.25	0.43
	(F) Pomatiopsidae (sm snail)	–	–	–	0	0.07	0.05	0	0.01	0.08
	(F) Gerridae (water strider)	–	–	–	0	0.01	0.08	0	0.02	0.08
	(F) Acrididae (grasshopper)	–	–	–	0	0.55	0.70	0.48	0.60	0.75
	Algae	–	–	–	0	0.01	0.05	0	0.01	0.05
	CPOM	–	–	–	0	0.00	0.03	0	0.08	0.05
A. dahli	(F) Hyriidae (mussel)	0.10	0.17	0.25	–	–	–	–	–	–
	(F) Pomatiopsidae (sm snail)	0	0.06	0.25	–	–	–	–	–	–
	(F) Gerridae (water strider)	0.55	0.71	0.85	–	–	–	–	–	–
	Algae**	0	0.04	0.15	–	–	–	–	–	–
	M. argentea (silver cadjeput)	0	0.01	0.05	–	–	–	–	–	–
	FPOM	0	0.01	0.05	–	–	–	–	–	–
	CPOM	0	0.01	0.08	–	–	–	–	–	–
N. hyrtlii	(F) Hyriidae (mussel)	0	0.09	0.07	–	–	–	–	–	–
	(F) Pomatiopsidae (sm snail)	0	0.29	0.22	–	–	–	–	–	–
	(F) Gerridae (water strider)	0.05	0.55	0.93	–	–	–	–	–	–
	Algae**	0	0.06	0.05	–	–	–	–	–	–
	FPOM	0	0.02	0.02	–	–	–	–	–	–
S. kreffti	*N. erebi* <100	–	–	–	0.43	0.78	0.95	–	–	–
	N. erebi >100	–	–	–	0	0.03	0.13	0.98	0.99	1.00
	C. lentiginosus	–	–	–	0	0.15	0.55	0	0.02	0.03
	(F) Gerridae (water strider)	–	–	–	0	0.02	0.08	0	0	0
	(F) Acrididae (grasshopper)	–	–	–	0	0.03	0.13	0	0	0
	Algae	–	–	–	0	0.01	0.05	0	0	0
M. australis	(F) Gerridae (water strider)	0	0.12	0.38	0.73	0.87	0.98	0.60	0.76	0.93
	(F) Acrididae (grasshopper)	0.6	0.81	0.98	0	0.06	0.13	0.05	0.18	0.04
	Algae	–	–	–	0	0	0	0	0.01	0.01
	FPOM	0	0.03	0.10	0	0	0	0	0.02	0.02
	CPOM	0	0.05	0.18	0.03	0.08	0.15	0	0.05	0.05
C. lentiginosus	(F) Pomatiopsidae (sm snail)	0	0.00	0.03	0	0.04	0.15	0	0.30	0.70
	(F) Sphaeriidae (pea clam)	–	–	–	0.48	0.66	0.78	0	0.23	0.55
	(F) Gerridae (water strider)	0	0.01	0.03	0	0.04	0.15	0	0.05	0.23
	(F) Acrididae (grasshopper)	0.98	0.99	1.00	0.10	0.26	0.48	0.20	0.39	0.53
	Algae	–	–	–	0	0.01	0.05	0	0.01	0.05
	FPOM	0	0	0	0	0.01	0.05	0	0.01	0.05
	CPOM	0	0	0	0	0.01	0.05	0	0.02	0.10
Ambassis sp.1	*C. lentiginosus*	0.73	0.78	0.83	0.78	0.89	0.98	0.03	0.06	0.10
	M. spinipes	0	0.06	0.13	0	0.07	0.20	0.90	0.94	0.98
	(F) Gerridae (water strider)	0	0	0	0	0.02	0.08	0	0	0
	(F) Acrididae (grasshopper)	0.15	0.17	0.20	0	0.02	0.08	0	0	0
	Algae	–	–	–	0	0.01	0.05	0	0	0
	CPOM	0	0	0	0	0.01	0.05	0	0	0
L. calcarifer	*N. erebi* <100	0.35	0.58	0.80	0	0.07	0.20	–	–	–
	N. erebi >100	0	0.04	0.13	0	0.04	0.13	0	0.21	0.14
	N. graeffei <150	0.05	0.29	0.53	0	0.15	0.48	–	–	–
	N. graeffei >150	–	–	–	0.43	0.63	0.83	0.30	0.48	0.07
	M. spinipes	0	0.09	0.25	0	0.12	0.40	0	0.32	0.68
A. percoides <40	*C. lentiginosus*	–	–	–	0.28	0.60	0.88	0.38	0.72	0.93
	G. giuris <70	–	–	–	0	0.16	0.60	0	0.15	0.55
	(F) Pomatiopsidae (sm snail)	–	–	–	0	0.04	0.18	0	0.04	0.15
	(F) Sphaeriidae (pea clam)	–	–	–	0	0.12	0.33	0	0.04	0.13
	(F) Gerridae (water strider)	–	–	–	0	0.03	0.15	0	0.02	0.08
	(F) Acrididae (grasshopper)	–	–	–	0	0.04	0.15	0	0.04	0.13
	Algae	–	–	–	0	0.01	0.08	0	0.00	0.03
	FPOM	–	–	–	0	0.01	0.08	0	0.00	0.03

Table 7 (cont.)

Consumer	Food sources	Wet season			Early dry season			Late dry season		
		1st	mean	99th	1st	mean	99th	1st	mean	99th
A. percoides >40	*C. lentiginosus*	0	0.18	0.50	0.73	0.83	0.90	0.73	0.87	0.98
	G. giuris <70	0	0.34	0.63	0	0.05	0.18	0	0.06	0.25
	(F) Pomatiopsidae (sm snail)	0	0.01	0.05	0	0.01	0.05	0	0.01	0.05
	(F) Sphaeriidae (pea clam)	–	–	–	0	0.01	0.05	0	0.01	0.05
	(F) Gerridae (water strider)	0	0.01	0.08	0	0.01	0.08	0	0.01	0.03
	(F) Acrididae (grasshopper)	0.35	0.45	0.55	0.03	0.10	0.18	0	0.05	0.20
	Algae**	0	0.01	0.03	0	0.01	0.05	0	0	0
	FPOM	0	0.01	0.05	0	0.00	0.03	0	0	0
H. greenwayi	*N. erebi* <100	–	–	–	0.80	0.80	0.80	–	–	–
	C. lentiginosus	–	–	–	0	0	0	–	–	–
	(F) Gerridae (water strider)	–	–	–	0	0	0	–	–	–
	Algae	–	–	–	0	0	0	–	–	–
	E. camaldulensis (river gum)	–	–	–	.03	.04	.05	–	–	–
	M. argentea (silver cadjeput)	–	–	–	0.15	0.16	0.18	–	–	–
	P. aquaticus (pandanus)	–	–	–	0	0	0	–	–	–
	FPOM	–	–	–	0	0	0	–	–	–
	CPOM	–	–	–	0	0	0	–	–	–
H. jenkinsi	*N. erebi* <100	0	0.31	0.73	0.03	0.41	0.75	–	–	–
	N. erebi >100	0	0.28	0.68	0	0.04	0.18	0.55	0.83	0.98
	N. graeffei <150	0	0.07	0.28	0	0.27	0.63	–	–	–
	C. lentiginosus	0	0.13	0.45	0	0.18	0.68	0	0.12	0.43
	(F) Sphaeriidae (pea clam)	–	–	–	0	0.04	0.18	0	0.01	0.05
	(F) Gerridae (water strider)	0	0.06	0.25	0	0.02	0.10	0	0.01	0.03
	(F) Acrididae (grasshopper)	0	0.05	0.23	0	0.04	0.18	0	0.04	0.15
	Algae**	0	0.02	0.10	0	0.01	0.08	0	0	0
	M. argentea (silver cadjeput)	0	0.06	0.20	0	0.01	0.08	0	0	0
	CPOM	0	0.04	0.18	0	0.01	0.08	0	0.00	0.03
L. unicolor	*N. erebi* <100	0	0.00	0.03	0	0.12	0.38	–	–	–
	C. lentiginosus	0	0.06	0.23	0	0.12	0.43	0	0.08	0.33
	G. giuris <70	0.05	0.26	0.40	0	0.07	0.28	0	0.04	0.18
	M. spinipes	0	0.03	0.10	0	0.41	0.78	0.43	0.62	0.78
	(F) Pomatiopsidae (sm snail)	0	0	0	0	0.03	0.15	0	0.02	0.08
	(F) Gerridae (water strider)	0	0	0	0	0.05	0.20	0	0.02	0.08
	(F) Acrididae (grasshopper)	0.48	0.65	0.70	0	0.19	0.48	0.10	0.23	0.33
	Algae**	0	0.01	0.05	0	0.03	0.13	0	0.01	0.08
G. aprion	*N. erebi* <100	0	0.17	0.48	0	0.32	0.70	–	–	–
	C. lentiginosus	0.05	0.54	0.88	0	0.25	0.78	0	0.22	0.73
	A. percoides <40	–	–	–	0	0.22	0.75	0	0.28	0.78
	(F) Sphaeriidae (pea clam)	–	–	–	0	0.05	0.20	0	0.26	0.58
	(F) Gerridae (water strider)	0	0.08	0.23	0	0.05	0.20	0	0.11	0.40
	(F) Acrididae (grasshopper)	0	0.22	0.48	0	0.10	0.30	0	0.09	0.35
	Algae	–	–	–	0	0.03	0.13	0	0.04	0.15
T. kimberleyensis <50	*Ambassis* sp.1	0	0.43	0.75	–	–	–	0	0.20	0.60
	M. spinipes	0	0.34	0.90	–	–	–	0	0.35	0.68
	(F) Pomatiopsidae (sm snail)	0	0.12	0.28	–	–	–	0	0.09	0.28
	(F) Gerridae (water strider)	0	0.08	0.28	–	–	–	0	0.10	0.33
	(F) Acrididae (grasshopper)	0	0.03	0.13	–	–	–	0.10	0.27	0.40
T. kimberleyensis >50	*Ambassis* sp.1	0.63	0.82	0.98	0	0.03	0.10	0	0.08	0.30
	M. spinipes	0	0.08	0.28	0.55	0.66	0.73	0.48	0.64	0.80
	(F) Pomatiopsidae (sm snail)	0	0.01	0.05	0	0.00	0.03	0	0.03	0.13
	(F) Gerridae (water strider)	0	0.01	0.05	0	0.01	0.03	0	0.03	0.13
	(F) Acrididae (grasshopper)	0	0.10	0.20	0.28	0.31	0.35	0.10	0.23	0.40

Consumer	Food sources	Wet season			Early dry season			Late dry season		
		1st	mean	99th	1st	mean	99th	1st	mean	99th
O. selheimi	*N. erebi* <100	0	0.01	0.08	–	–	–	–	–	–
	N. erebi >100	0	0.01	0.05	–	–	–	–	–	–
	C. lentiginosus	0	0.09	0.35	–	–	–	–	–	–
	Ambassis sp.1	0.10	0.55	0.88	–	–	–	–	–	–
	G. giuris <70	0	0.18	0.73	–	–	–	–	–	–
	M. spinipes	0	0.13	0.53	–	–	–	–	–	–
	(F) Pomatiopsidae (sm snail)	0	0.02	0.08	–	–	–	–	–	–
	(F) Gerridae (water strider)	0	0.03	0.13	–	–	–	–	–	–
G. giuris <70	*N. erebi* <100	0	0.04	0.13	0.03	0.43	0.73	–	–	–
	C. lentiginosus	0.40	0.72	0.95	0	0.09	0.35	0	0.19	0.70
	A. percoides <40	–	–	–	0	0.24	0.78	0	0.15	0.50
	G. aprion	0	0.16	0.55	0	0.01	0.08	0.05	0.53	0.88
	(F) Gerridae (water strider)	0	0.01	0.08	0	0.19	0.33	0	0.11	0.28
	(F) Acrididae (grasshopper)	0	0.07	0.18	0	0.02	0.03	0	0.02	0.10
	Algae	–	–	–	0	0.05	0.18	0	0.02	0.05
G. giuris >70	*N. erebi* <100	0	0.08	0.28	–	–	–	–	–	–
	C. lentiginosus	0.03	0.48	0.88	–	–	–	–	–	–
	G. aprion	0	0.28	0.88	–	–	–	–	–	–
	(F) Gerridae (water strider)	0	0.04	0.15	–	–	–	–	–	–
	(F) Acrididae (grasshopper)	0	0.13	0.33	–	–	–	–	–	–

** Despite no filamentous algae being collected during the wet season, the isotopic signature of filamentous algae collected in the early dry season was substituted for use in IsoSource analysis, for those species where algae was recognised as a significant dietary prey item.

IsoSource agreed with dietary data that aquatic arthropods were important prey for smaller *N. erebi* in some seasons, the major energy source of both large and small *N.erebi* may be of molluscan origin.

Six species were caught in very low numbers and often had stomachs that were either almost or entirely empty. Of these species, the major content of *Elops hawaiensis* was ~40% biofilm/silt/sand and algae, and ~60% insects, those of *Megalops cyprinoides* were ~85% insects and ~15% fish, and those of *Hannia greenwayi* were 65% algae, 10% hemipterans and 25% fish (Table 4). In contrast to dietary analyses, *IsoSource* modeling indicated that fish were the most important component of the diets of these species (Table 7), with insects only being the most important item for *E. hawaiensis* during the wet season. In the cases of *Strongylura krefftii* and *Neosilurus hyrtlii*, the stomach contents and *Isosource* modeling were in accord in that both indicated that *S. krefftii* is a piscivore that includes a small proportion of aquatic insects in its diet, whereas *N. hyrtlii* feeds almost exclusively on aquatic snails and arthropods. The remaining species, *Oxeleotris selheimi*, never contained anything in its stomach but *IsoSource* indicated that fish made up the vast majority of its diet.

Differences in diets between size categories

The stomach contents of five species, i.e. *N. erebi, N. graeffei, A. percoides, T. kimberleyensis* and *G. giuris* differed between size classes in at least one season (Tables 1–3, 5). For example, during the wet season although *N. erebi* <100 mm and >100 mm both consumed large quantities of biofilm/silt, individuals >100 mm also consumed a large amount of vegetation (~13%). During the early dry season the stomach contents of the smaller fish were dominated by aquatic invertebrates (~88%), whereas larger fish continued to consume soil/silt (~70%) and vegetation (~29%). In the cases of *N. graeffei* and *T. kimberleyensis,* smaller fish consumed far larger quantities of aquatic invertebrates than terrestrial invertebrates (47–86% cf. 9–19%), whilst the opposite was the case for larger individuals (10–30% cf. 41–75%). Large and small individuals of *G. giuris* consumed large quantities of aquatic invertebrates (58–100%), however, larger individuals also ingested terrestrial invertebrates and aquatic vegetation as well as more fish. The stomach contents of *A. percoides* <40 mm consisted almost entirely of aquatic invertebrates whereas those of larger fish also contained large amounts of aquatic vegetation (17–53%).

Differences and overlap in diets within a season

Within the wet season (Figure 1, Tables 1, 5, 8), classification of mean dietary data identified four major feeding groups. Group 1 was comprised of *N. erebi* <100 mm and *N. erebi* >100 mm on the basis that they consumed biofilm/silt. Group 2 contained the greatest number of species, all of which consumed large quantities of aquatic insects, in particular aquatic hemipterans. Four subgroups (I–IV) were identified within Group 2. Subgroup I (*M. australis* and *T. kimberleyensis* 50–110 mm) also consumed a substantial volume of terrestrial hymenopterans and arachnids. Members of Subgroup II included *G. giuris* <70 mm, *T. kimberleyensis* <50 mm, *C. lentiginosus* and *Ambassis* sp. 1 whose diets were dominated by dipteran pupae. Species in Subgroup III (*G. aprion* and *G. giuris* >70 mm) were the only species that consumed a large proportion of teleost prey in Group 2, whilst fishes in Subgroup IV (*A. percoides* >40 mm, *N. graeffei* <150 mm and *L. unicolor*) commonly consumed large amounts of filamentous algae.

Lates calcarifer was the only species constituting Group 3, had a diet largely of teleost prey and *Macrobrachium spinipes* and had a diet significantly different to all other species. Group 4 included *N. graeffei* >150 mm and *H. jenkinsi* and were separated on the basis that the diet contained terrestrial vegetation and fig/fruit, with ANOSIM indicating that the diet of *N. graeffei* was significantly different to all other species except *H. jenkinsi*. There was also some overlap between *H. jenkinsi* and *L. unicolor*. ANOSIM suggested that the diets of both large and small *N. erebi* were significantly different to all other species, but were not significantly different to each other. Within Group 2, ANOSIM suggested that there were no significant differences in the prey consumed by the species within each subgroup. There were, however, differences between species in one subgroup when compared to those in another.

Classification of mean dietary data collected in the early dry season (Figure 2, Tables 2, 5, 9) revealed seven major feeding groups. The diet of Group 1 (*N. erebi* <100 mm) was made up almost entirely of cladocerans and copepods and this group had a diet significantly different to all other species. Group 2 (*P. pristis*, *L. calcarifer* and *C. leucas*) consumed a high proportion of fish, with significant differences found between *L. calcarifer* and both *P. pristis* and *C. leucas* only. Filamentous algae and biofilm/silt were major components of the diet in *N. erebi* (>100 mm), the single member of Group 3 and this was significantly different to all others. Group 4 (*M. australis*, *A. percoides* >70 and *H. jenkinsi*) consumed a large proportion of filamentous algae. Group 5 included species that consumed a high proportion of dipteran and ephemeropteran larvae, with *C. lentiginosus* different to all other species across all groups, while *A. percoides* (<40 mm) was different to all other species, except *G. giuris*. The species in Group 6 (i.e. *L. unicolor*, *Ambassis* sp. 1, *N. graeffei* <150 and *G. aprion*) consumed a broad range of aquatic invertebrates and exhibited considerable dietary overlap. Those in Group 7 (*N. graeffei* >150 and *T. kimberleyensis*) were separated on the basis that they consumed mainly terrestrial insects.

Classification of mean dietary data collected in the late dry season (Figure 3, Tables 3, 5, 10) recognised five major feeding groups. Group 1 (*N. erebi* >100 mm and *P. pristis*) diets were dominated by detritus but as *P. pristis* also consumed teleosts each species diets were significantly different. Group 2 (*C. leucas* and *L. calcarifer*) diets contained a large proportion of fish and were not significantly different to each other. *Lates calcarifer* diets were significantly different to all other species. The fish in Group 3 (*N. graeffei* >150 mm and *T. kimberleyensis* >50 mm) were separated from other groups on the basis that they consumed higher quantities of terrestrial insects. While their diets were not significantly different to each other, they were generally significantly different to most other species. The fish in Group 4 (i.e. *M. australis* and *H. jenkinsi*) consumed a large portion of filamentous algae, in addition to a number of aquatic insects. The stomach contents of these species were significantly different to all other species, but were not significantly different to each other. Group 5 contained the remaining eight species, all of which had ingested a range of smaller aquatic invertebrates and on many occasions there were significant differences between the prey consumed between these species and those in other groups.

Overall, the highest dietary overlap was observed in the wet season when 30% (i.e. 36 of 120) of the dietary pairwise comparisons between species (and size classes) were not significantly different (Table 8). Overlap then decreased to 20% in the early dry season (i.e. 21 of the 105 pairwise comparisons were similar) (Table 9) before rising to ~26% (24 of the 91) the late dry season (Table 10).

Stable isotope analyses – seasonal $\delta^{13}C$ and $\delta^{15}N$ signatures and trophic position

The variation in $\delta^{15}N$ (Table 6) and $\delta^{13}C$ values of insectivorous fishes in each season provides further indication of the seasonal variability in food sources and dependency by fishes upon them. For example, $\delta^{15}N$ signatures of a number of insectivores were lower in the late dry season than in the wet or early dry season. Furthermore, this feeding guild experienced greater variability in $\delta^{13}C$ and $\delta^{15}N$ signatures than piscivores, terrestrial insectivores and detritivores.

$\delta^{13}C$ and $\delta^{15}N$ analysis provided some clarification of the feeding habits of several species, including several of those poorly represented by dietary analysis. For example, analysis of *E. hawaiensis* and *M. cyprinoides* indicated $\delta^{15}N$ values of a piscivorous diet. Similarly, *H. jenkinsi* and *H. greenwayi*, which were considered to be detritivores/algivores from stomach content analysis, had $\delta^{15}N$ values closer to, and indeed above, that of insectivorous fishes, indicating a greater importance in higher order food types such as invertebrates and/or fishes, than the algae consumed. Stomach content analysis revealed the consumption of cladocerans by small *N. erebi* (<100 mm TL) in the early dry season rather than detritus. The assimilation of a higher order prey source in the tissues determined by isotopic analyses indicated the importance of cladocerans in the diet and growth of small *N. erebi*.

Stable isotope analyses – assimilation of food sources in fishes of the Fitzroy River

Stomach content analysis indicates that a large number of the fish species collected from the Fitzroy River would be considered insectivores. This was indeed the case for *Ambassis* sp. 1, *A. percoides*, *L. unicolor*, *G. aprion*, *T. kimberleyensis*, *O. selheimi* and *G. giuris*. While *IsoSource* supports the prevalence of insects in the diets of these fishes, isotope analysis also suggested that fishes and *M. spinipes*, although less frequently ingested (or rarely observed in the analysis of stomach content) may be equally, if not more, important than insects in terms of the energy that they provided to these species (Table 7). For example, while terrestrial Orthoptera appeared to be the main food source of *E. hawaiensis* in the wet season, the fishes *C. lentiginosus* and small *N. erebi* (<100 mm TL) appeared to be the most important prey in the early dry season. These latter prey species plus *Ambassis* sp. 1, were apparently also the main source of energy to *M. cyprinoides* in the wet season, while larger *N. erebi* appeared to provide this energy in the late dry. Indeed, they provide between 55 and 95% of the energy to the species in that season.

Despite vast quantities of filamentous algae being recorded from the diets of *N. erebi* >100 mm TL, *IsoSource*

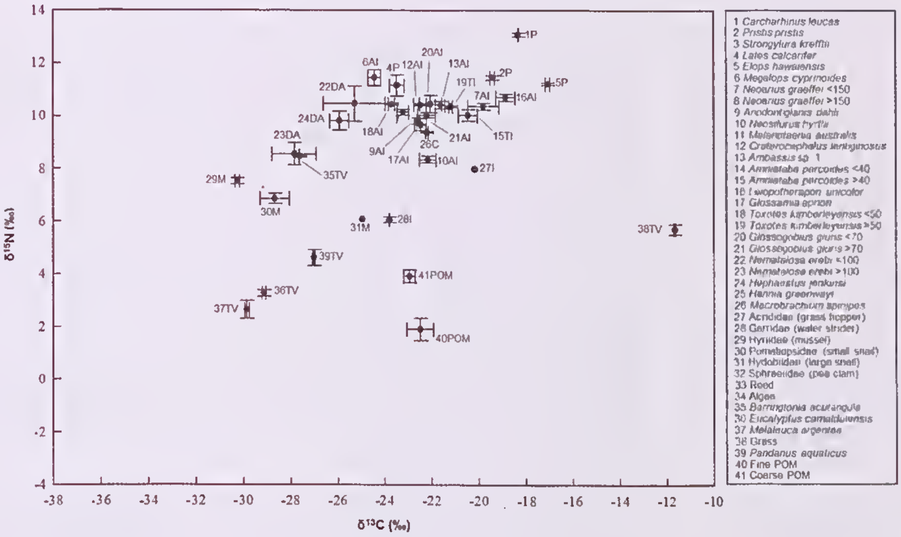

Figure 4 The isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) (‰) of the different fish, insects, molluscs, vegetation and organic matter samples collected from the Fitzroy River during the wet season. Species categorisations for comparative purposes are based on dietary analyses undertaken during the current study, Bishop *et al.* (2001) and Allen *et al.* (2002) (POM: Particulate organic matter, TV: Terrestrial vegetation, AV: Aquatic vegetation, M: Mollusc, I: Insect, C: Crustacean, DA: Detritivore/ Algivore, AI: Aquatic Insectivore, TI: Terrestrial Insectivore, P: Piscivore).

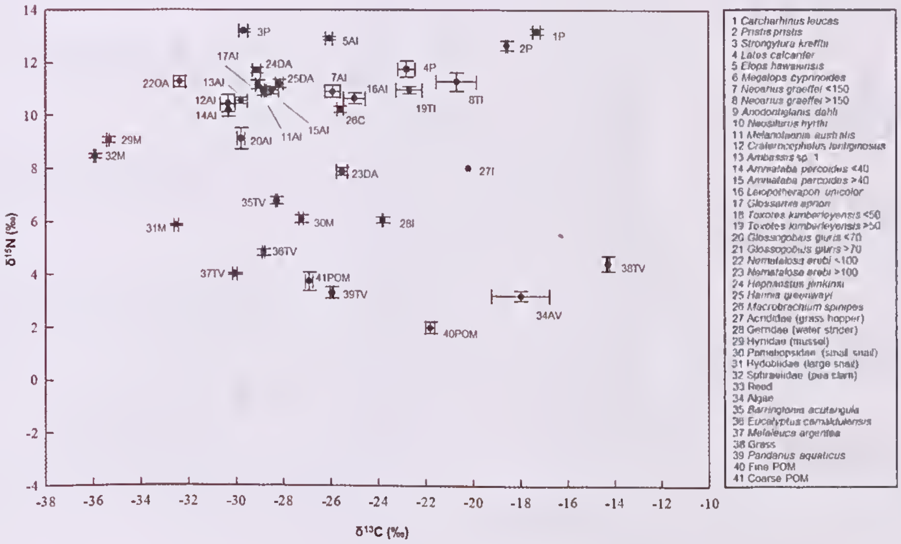

Figure 5 The isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) (‰) of the different fish, insects, molluscs, vegetation and organic matter samples collected from the Fitzroy River during the early dry. Species categorisations for comparative purposes are based on dietary analyses undertaken during the current study, Bishop *et al.* (2001) and Allen *et al.* (2002) (POM: Particulate organic matter, TV: Terrestrial vegetation, AV: Aquatic vegetation, M: Mollusc, I: Insect, C: Crustacean, DA: Detritivore/ Algivore, AI: Aquatic Insectivore, TI: Terrestrial Insectivore, P: Piscivore).

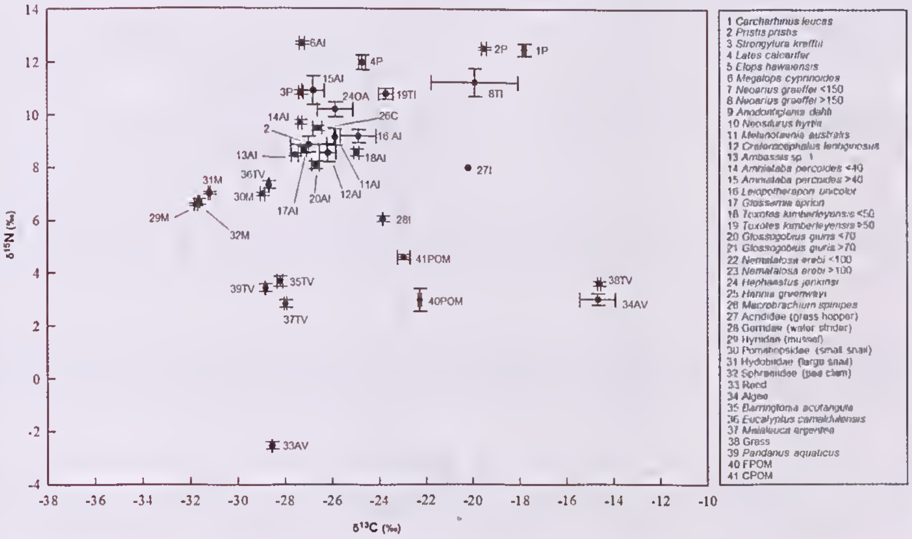

Figure 6 The isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) (‰) of the different fish, insects, molluscs, vegetation and organic matter samples collected from the Fitzroy River during the late dry season Species categorisations for comparative purposes are based on dietary literature by analyses undertaken during the current study, Bishop *et al.* (2001) and Allen *et al.* (2002) (POM: Particulate organic matter, TV: Terrestrial vegetation, AV: Aquatic vegetation, M: Mollusc, I: Insect, C: Crustacean, DA: Detritivore/Algivore, AI: Aquatic Insectivore, TI: Terrestrial Insectivore, P: Piscivore).

Table 8 R-statistic values for pairwise ANOSIM comparisons of the diets of fish species examined from freshwaters of the Fitzroy River in the wet season. Significant dietary differences are represented by * where $p<0.05$ and **$p<0.01$ and R-stat >0.300. Global R = 0.430. See Table 1 for species codes.

Species	*Ne* <100	*Ne* >100	*Ng* <150	*Ng* >150	*Ma*	*Cl*	*Am*	*Lc*	*Ap* >40	*Hj*	*Lu*	*Ga*	*Tk* <50	*Tk* 50–110	*Gg* <70
Ne >100	0.001	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ag <150	0.866**	0.937**	–	–	–	–	–	–	–	–	–	–	–	–	–
Ag >150	0.860**	0.853**	0.606**	–	–	–	–	–	–	–	–	–	–	–	–
Ma	0.493**	0.636**	0.246	0.593**	–	–	–	–	–	–	–	–	–	–	–
Cl	0.528**	0.660**	0.340**	0.669**	0.267	–	–	–	–	–	–	–	–	–	–
Am	0.460**	0.632**	0.217	0.647**	0.241	0.049	–	–	–	–	–	–	–	–	–
Lc	0.458**	0.568**	0.390**	0.435**	0.412**	0.419**	0.390**	–	–	–	–	–	–	–	–
Ap >40	0.502**	0.475**	0.049	0.592**	0.396**	0.380**	0.348**	0.464**	–	–	–	–	–	–	–
Hj	0.584**	0.582**	0.201	0.276	0.529**	0.555**	0.518**	0.430**	0.206	–	–	–	–	–	–
Lu	0.371**	0.460**	0.046	0.456**	0.153	0.186	0.169	0.321**	0.100	0.240	–	–	–	–	–
Ga	0.785**	0.849**	0.619**	0.799**	0.288	0.209	0.306**	0.451**	0.438**	0.670**	0.120	–	–	–	–
Tk <50	0.822**	0.913**	0.313**	0.716**	0.121	0.069	0.039	0.441**	0.331**	0.608**	0.002	0.245	–	–	–
Tk 50–110	0.891**	0.938**	0.579**	0.363**	0.096	0.334**	0.344**	0.458**	0.489**	0.569**	0.121	0.389**	0.271	–	–
Gg <70	0.785**	0.859**	0.581**	0.816**	0.429**	0.071	0.273	0.537**	0.484**	0.686**	0.364**	0.544**	0.398**	0.649**	–
Gg >70	0.786*	0.925**	0.236	0.704**	0.200	0.198	0.199	0.306**	0.343**	0.486**	0.010	0.177	0.129	0.324**	0.574**

Table 9 R-statistic values for pairwise ANOSIM comparisons of the diets of fish species examined from freshwaters of the Fitzroy River in the early dry season. Significant dietary differences are represented by * where $p<0.05$ and **$p<0.01$ and R-stat >0.300. Global R = 0.547. See Table 1 for species codes.

Species	*Cle*	*Pp*	*Ne* <100	*Ne* >100	*Ng* <150	*Ng* >150	*Ma* >40	*Cl*	*Am*	*Lc*	*Ap* <40	*Ap* >70	*Hj*	*Lu*	*Ga*	*Tk* >50
Pp	0.370*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ne <100	0.629**	0.575**	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ne >100	0.963**	0.976**	0.886**	–	–	–	–	–	–	–	–	–	–	–	–	–
Ag <150	0.712**	0.700**	0.707**	0.937**	–	–	–	–	–	–	–	–	–	–	–	–
Ag >150	0.718**	0.603**	0.692**	0.811**	0.368**	–	–	–	–	–	–	–	–	–	–	–
Ma >40	0.534**	0.384**	0.305**	0.616**	0.230	0.415**	–	–	–	–	–	–	–	–	–	–
Cl	0.851**	0.874**	0.743**	0.937**	0.705**	0.702**	0.557**	–	–	–	–	–	–	–	–	–
Am	0.403**	0.322**	0.406**	0.775**	0.127	0.458**	0.285	0.495**	–	–	–	–	–	–	–	–
Lc	0.093	0.298	0.657**	0.868**	0.678**	0.690**	0.589**	0.781**	0.537**	–	–	–	–	–	–	–
Ap <40	0.813**	0.837**	0.720**	0.937**	0.678**	0.662**	0.475**	0.545**	0.466**	0.747**	–	–	–	–	–	–
Ap >70	0.753**	0.883**	0.480**	0.926**	0.575**	0.529**	0.015	0.782**	0.140	0.682**	0.760**	–	–	–	–	–
Hj	0.933**	0.794**	0.834**	0.814**	0.749**	0.632**	0.232	0.898**	0.557**	0.788**	0.888**	0.370**	–	–	–	–
Lu	0.560**	0.423**	0.527**	0.682**	0.041	0.335**	0.170	0.474**	0.147	0.610**	0.376**	0.056	0.315**	–	–	–
Ga	0.339**	0.250	0.451**	0.746**	0.022	0.344**	0.216	0.440**	0.079	0.462**	0.344**	0.180	0.514**	0.034	–	–
Tk >50	0.688**	0.703**	0.638**	0.933**	0.480**	0.259	0.263	0.811**	0.339**	0.684**	0.770**	0.689**	0.831**	0.480**	0.317**	–
Gg	0.486**	0.456**	0.448**	0.785**	0.385**	0.503**	0.329**	0.479**	0.291	0.558**	0.044	0.389**	0.659**	0.242	0.239	0.512**

Table 10 R-statistic values for pairwise ANOSIM comparisons of the diets of fish species examined from freshwaters of the Fitzroy River in the late dry season. Significant dietary differences are represented by * where $p<0.05$ and **$p<0.01$ and R-stat >0.300. Global R = 0.558. See Table 1 for species codes.

Species	*Cle*	*Pp*	*Ne* >100	*Ng* >150	*Ma*	*Cl*	*Am*	*Lc*	*Ap* 40–70	*Ap* >70	*Hj*	*Lu*	*Ga*	*Tk* <50	*Tk* >50
Pp	0.345	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ne >100	0.996*	0.433**	–	–	–	–	–	–	–	–	–	–	–	–	–
Ag >150	0.196	0.097	0.639**	–	–	–	–	–	–	–	–	–	–	–	–
Ma	0.966**	0.975**	0.907**	0.396**	–	–	–	–	–	–	–	–	–	–	–
Cl	0.903**	0.911**	0.912**	0.435**	0.672**	–	–	–	–	–	–	–	–	–	–
Am	0.609**	0.611**	0.928**	0.322**	0.800**	0.452**	–	–	–	–	–	–	–	–	–
Lc	0.019	0.480*	0.917**	0.409**	0.855**	0.823**	0.695**	–	–	–	–	–	–	–	–
Ap 40–70	0.635**	0.640**	0.887**	0.211	0.566**	0.533**	0.293	0.708**	–	–	–	–	–	–	–
Ap >70	0.764**	0.804*	0.962**	0.098	0.774**	0.331**	0.382**	0.742**	0.193	–	–	–	–	–	–
Hj	0.787**	0.815**	0.872**	0.185**	0.270	0.636**	0.732**	0.728**	0.458**	0.582**	–	–	–	–	–
Lu	0.542**	0.564**	0.943**	0.219**	0.794**	0.564**	0.286	0.649**	0.125	0.222	0.702**	–	–	–	–
Ga	0.011	0.031	0.785**	0.158	0.558**	0.406**	0.160	0.310**	0.095	0.061	0.399**	0.010	–	–	–
Tk <50	0.926**	0.948**	0.993**	0.307**	0.818**	0.657**	0.457**	0.791**	0.444**	0.854**	0.887**	0.202	0.058	–	–
Tk >50	0.737**	0.761*	0.984**	0.022	0.796**	0.866**	0.552	0.739**	0.573**	0.760**	0.835**	0.494**	0.150	0.571**	–
Gg <70	0.412**	0.444*	0.848**	0.307**	0.648**	0.201	0.139	0.556**	0.150	0.202	0.591**	0.146	0.089	0.197	0.431**

indicated that a higher calorific taxa (in this case molluscs) may be of much greater importance in the diet of this species than indicated by stomach contents analysis. A similar situation is also apparent for small *N. erebi, H. jenkinsi* and *H. greenwayi*. The energy assimilated by the first of these species may be derived from aquatic invertebrates (a result supported by stomach content analysis), whereas in the other two species much of their energy appears to be derived from fishes.

IsoSource also indicated seasonal shifts between energetically favourable food types. For example, while terrestrial insects were the most important food source of small *N. graeffei* (<150 mm TL) in the wet season, fishes (*C. lentiginosus* and *G. giuris* <70 mm TL) and *M. spinipes* were also assimilated. In contrast, insects appeared less important in the diet of small *N. graeffei* in the early dry season, when a greater proportion of fishes, in particular small *N. erebi, C. lentiginosus* and *G. giuris* (<70 mm TL), were consumed.

Stomach content analysis indicated that *N. erebi* and *N. graeffei* were important prey for the piscivorous *C. leucas, P. pristis* and *L. calcarifer*. Although the current study supported this finding for the latter species, *IsoSource* suggested that *P. pristis* is the most energetically important prey source of *C. leucas* in all seasons.

DISCUSSION

Stomach content analyses of fishes of the Fitzroy River were generally consistent with the few data available from other systems in tropical Australia (e.g. Pusey *et al.* 2000; Morgan *et al.* 2004a; Davis *et al.* 2010, 2013). However, stable isotope analysis indicated that the food resource most frequently encountered during stomach content analysis may not be the most energetically important prey resource of that species and indeed may not accurately depict the 'dietary' guild to which it has historically been assigned. Stable isotope analysis indicated that the freshwater fish fauna of northern Australia may not differ as markedly as previously believed to those of Asia, Africa and South America. In the latter systems, terrestrial plant material, insects (aquatic and terrestrial) and detritus are major direct food sources for many fishes and these communities generally also support a diverse and abundant range of piscivores (Lowe-McConnell 1987). While insects were observed to be of particular importance to the freshwater fishes of the Fitzroy River, stable isotope analysis revealed that fish may also be an energetically important food source for a majority of the species present.

Diets of the fishes collected from the Fitzroy River showed some consistency with published accounts of the diets of these species from other river systems in northern Australia and confirmed the importance of aquatic insects as a food source in tropical freshwater systems (Angermeier & Karr 1983; Bishop *et al.* 1986, 2001; Pusey *et al.* 2000, 2004; Morgan *et al.* 2004a; Davis *et al.* 2010, 2013). Nevertheless, differences to published accounts were observed for a number of species. For example, although *A. percoides* and *M. australis* are commonly regarded as carnivorous elsewhere in Australia, filamentous algae was the single largest food type consumed by *A. percoides* in all seasons in the Fitzroy River and by *M. australis* in the early and late dry seasons. While filamentous algae was reported to be the major food consumed by *L. unicolor* in Lake Kununurra (Morgan *et al.* 2004a), in the Fitzroy River, this species ingested very little filamentous algae and fed almost exclusively on aquatic insects (see also Davis *et al.* 2010). Terrestrial insects, in particular orthopterans and coleopterans, were a major prey item of *N. graeffei* in the Fitzroy River, whereas they were only minor contributors to the diet of this species captured elsewhere (Morgan *et al.* 2004a). The diet of *G. aprion* in the Fitzroy River (and in Lake Kununurra (Morgan *et al.* 2004a)) was dominated by aquatic insects (especially aquatic hemipterans), whereas this species has been reported to consume high proportions of fish and macro-crustaceans elsewhere in Australia (Bishop *et al.* 2001).

Ontogenetic changes in the diets of Fitzroy River fishes

Approximately half of the freshwater fishes collected from the Fitzroy River during this study demonstrated some degree of ontogenetic change in their diet, i.e. *N. erebi, N. graeffei, A. percoides, T. kimberleyensis* and *G. giuris*. The current study indicated that a number of factors, other than a physical ability to swallow a prey, are responsible for these changes in diet. As noted by Schmitt & Holbrook (1984) variation in the diets of different sized fishes may be influenced by habitat utilisation, foraging behaviours and feeding rates, in addition to size-related morphological constraints. Changes in food utilisation may be observed as a 'shift' in the food items consumed at a particular stage in ontogeny or as a gradual increase in the size (and type) of food items ingested as the fish grows. Changes in the diet associated with major morphological developments and/or changes in habitat utilisation often result in abrupt and major changes in diet, whereas changes with growth may be less abrupt and often include an overall broadening of the diet (see for example Hyndes *et al.* 1997; Gill & Morgan 1998, 2003; Huskey & Turingan 2001; Cocheret de la Morinière *et al.* 2003; Nunn *et al.* 2007a, 2007b; Davis *et al.* 2010).

During this study, smaller *N. graeffei* <150 mm were shown to consume relatively large proportions of small aquatic invertebrates, while the diet of *N. graeffei* >150 mm was dominated by larger food items including terrestrial coleopterans and orthopterans, and during the wet season also figs. Frugivory of northern Australian terapontids was previously reported by Davis *et al.* (2010) at times of the year when this food type was available. An increase in the number of food types with growth (11 cf. 18 and 16 cf. 22 in the wet and early dry seasons, respectively) was also observed. Pusey *et al.* (1995) suggested that an increase in mouth gape was closely correlated to an increased reliance on terrestrial prey in fishes of tropical Australia. However, in the case of *N. graeffei* in the Fitzroy River, the ingestion of large food items with a terrestrial origin is also likely to be attributable to changes in foraging behaviours and the habitat utilised. An increase in size not only results in a food item 'fitting' the larger mouth, but also improves mobility and reduces the likelihood of predation thereby allowing utilisation of previously unavailable and/or dangerous habitats by larger individuals.

At the time of early dry season sampling, Geikie

Gorge was experiencing an apparent 'bloom' of cladocerans and copepods. During this period, the diet of small *N. erebi* was dominated by these microcrustaceans (~90%), whereas in larger *N. erebi* a similar proportion of the diet was made up of filamentous algae and biofilm/silt. During the wet season, the diets of both small and large *N. erebi* were comprised almost exclusively of filamentous algae and biofilm/silt.

In the case of *A. percoides*, *T. kimberleyensis* and *G. giuris*, the number of food types ingested by each of these individual species is roughly comparable between the small and large individuals. However, whilst the number of food types may be similar the categories that make up that number can vary considerably between the respective size groups. For example, in the early dry season small *A. percoides* consumed large quantities of small aquatic invertebrates, whereas the diets of large *A. percoides* consisted of algae, gastropods and ostracods. In the late dry season, when the smaller size group of *A. percoides* had increased from <40 mm to between 40 and 70 mm, their diet now not only included smaller aquatic invertebrates, but also a significant proportion of larger aquatic invertebrates such as odonatan and coleopteran larvae. In this season large *A. percoides* continued to ingest ostracods and also consumed a high proportion of odonatan larvae, but were no longer feeding on gastropods or filamentous algae to the same extent, which contrasts the study of Davis *et al.* (2010). This suggests that there is a progression of diet from small aquatic invertebrates to filamentous algae and larger and more robust aquatic invertebrates. This gradual change is indicative of an opportunistic omnivore that can optimise its diet dependent on its ability to ingest available food resources. The change to larger prey, such as odonatan larvae and more robust prey, including ostracods and gastropods, is likely to be attributable to an increase in gape size and the development and ossification of pharyngeal plates which aid in processing prey with a hard exoskeleton or shell.

Toxotes kimberleyensis also exhibited a 'shift' in diet from predominantly aquatic invertebrates to between 50 and 70% (dependent upon season) terrestrial and flying insects. Despite possessing the ability to spurt water from a very small size, the power generated by the muscles of the buccal floor can only force a low volume of water at a low pressure over a short distance (Vailati *et al.* 2012). Thus, transition to terrestrial prey in larger *T. kimberleyensis* is more likely attributed to the power, volume and accuracy of the jet that can be generated by larger fishes, than a physical ability for an individual to pass a prey beyond its jaws.

Glossogobius giuris, like *A. percoides* and *T. kimberleyensis*, exhibited a 'shift' in the diet between small and larger fish. Small *G. giuris* consumed a high proportion of ostracods, dipteran pupae and aquatic hemipterans. In contrast, larger *G. giuris* did not consume any ostracods or dipteran pupae, but consumed more aquatic hemipterans and also a significant proportion of large aquatic coleopterans, orthopterans and fish. None of these latter taxa were ingested by small *G. giuris*. As all sizes of *G. giuris* were captured within the same microhabitats (i.e. shallow bank waters over sandy substrates), differences in diet are presumably attributable to the ability of larger individuals to ingest larger prey items, rather than changes in foraging behaviour or habitat utilisation.

Energetically important food sources of the fishes of the Fitzroy River: Comparison of stomach contents analysis and stable isotope analysis

The Fitzroy River is considered comparatively 'rich' in terms of its fish diversity (Morgan *et al.* 2004b, 2011). The permanence of deep water throughout the year, extensive shallow littoral zones and dense riparian vegetation present in Geikie Gorge undoubtedly contribute to the abundant and diverse range of food types present. Despite the widespread consumption of filamentous algae, *IsoSource* suggested that energetically this food source may be of less importance than would be assumed from the large quantities ingested by many of the fishes. This finding supports those of Bunn *et al.* (1998, 1999, 2001) where filamentous algae and macrophytes were found to be an insignificant component of consumer food webs. Results of stomach content analysis during the current study, and findings by others (see Bishop *et al.* 2001; Allen *et al.* 2002), suggest that *N. erebi* is a detritivore/algivore. However, *IsoSource* indicated that pea clams were a very important source of assimilated energy as were aquatic invertebrates for small individuals in some seasons, a finding also reflected by dietary analysis. As small molluscs were rarely found in the diets of *N. erebi*, this result may be an overestimation of *Isosource* analysis due to the exclusion of a wide range of invertebrate taxa (see Methods section). However, energy is undoubtedly derived from taxa higher than biofilm/silt or algae. It is therefore possible that epiphytic micro-invertebrates present on filamentous algae have a signature closer to that of pea clams and it is these epiphytic invertebrates that provide energy to *N. erebi* and other apparent algal feeders. Support for this notion that algae is less energetically important in the diets of these species, is provided by isotopic studies on the Ord River, Western Australia (Trayler *et al.* 2003). For example, Trayler *et al.* (2003) revealed that filamentous algae and macrophytes were not significant contributors to consumer biomass or the food web but rather that non-filamentous benthic algae and an additional unknown algal source were.

Dietary analysis also indicated that small *N. erebi* (<100 mm TL) opportunistically fed on small invertebrates. The importance of this food source was confirmed by isotopic analysis which indicated that small *N. erebi* were far more enriched in $\delta^{15}N$ than larger individuals of this species. Numerous authors have suggested the ability of small individuals to utilise higher calorific prey items which result in high growth rates earlier in the life cycle and thereby lead to the rapid attainment of a size that provides both a competitive feeding advantage and the reduced risk of predation (Grossman 1980; Brown 1985; Wainright & Richard 1995; Huskey & Turingan 2001; Lima-Junior & Goitein 2003).

IsoSource indicated the widespread assimilation of fish in species occurring in the Fitzroy River. While complimentary results of dietary and stable isotope analysis confirmed the presence of three large piscivores (*C. leucas*, *P. pristis* and *L. calcarifer*), fish was identified as an important prey source to an additional 11 species, including *H. greenwayi* and *H. jenkinsi* which are generally considered to be algivores and *T. kimberleyensis* which is considered to be a strict insectivore.

Of particular note during the current study was that *IsoSource* suggested *P. pristis* is the most energetically important prey source of *C. leucas* in all seasons. *Pristis pristis* is protected in Australia under the EPBC *Act 1999* and listed as critically endangered by the International Union for Conservation of Nature (IUCN). Predation of *P. pristis* by *C. leucas* was reported from northern Australian rivers by Thorburn & Rowland (2008). Although these authors suggested that overall *P. pristis* represented only a small dietary contributor (~2.5% by volume), the comparatively high numbers of *P. pristis* occurring in the Fitzroy River as opposed to other rivers surveyed in northern Australia (see for example Thorburn *et al.* 2003, 2007) may suggest that *P. pristis* is a far greater prey source of *C. leucas* in this system than in the other rivers surveyed.

Dietary shifts, resource partitioning and overlap in the Fitzroy River

Despite some seasonal variation in prey abundances being reflected in the diets of individual species, few data supported the notion that the diets of each species were 'narrower' in times of low productivity. Dietary analysis indicated that 'shifts' or 'replacements' in the types of prey consumed were often made to 'functionally' similar prey types, for example, between different types of aquatic larvae, or between aquatic hemipterans and aquatic coleopterans. The lack of contrast may be attributed to the permanence of water in Geikie Gorge, relative stability of the available habitat and an apparent 'richness' in prey types and abundances. Much of the variation in fish diets is undoubtedly attributable to the hatching of aquatic and terrestrial insect larvae, coinciding with the wet season and early dry season (Zaret & Rand 1971; Angermeier & Karr 1983; Sumpton & Greenwood 1990; Bunn & Arthington 2002). Thus, the majority of species investigated during the current study had broad diets, were opportunistic in their feeding habits and showed little 'real' change in their diets between seasons. Such a conclusion is consistent with the results of Kennard (1995), who found little temporal variation in fish diets over an eight month monitoring period in the Normanby River, Queensland.

A main aim of this study was to investigate how dietary overlap varies between seasons and in response to changes in the availability of prey. Increase in dietary overlap can occur when food becomes very limited, when fish will have to consume any type of food that is available to them in order to survive (see Matthews 1988). However, overlap can also occur as a result of an abundance of prey sources, such as during the wet season, when fish can opportunistically consume any of the wide variety of foods present.

Although the magnitude of change in dietary overlap between seasons was relatively small during the current study, dietary overlap was higher in the wet season (no dietary difference existed in ~30% of pairwise comparisons) and became reduced in the early dry season (no dietary difference existed in ~20% of pairwise comparisons) possibly reflecting the contraction of food resources and the return of fishes to more specialised feeding behaviours, as hypothesised. Overlap was again shown to increase in the late dry season (no dietary difference existed in ~26% of pairwise comparisons). The reasons behind this small magnitude of change may be attributed to two possible factors. Firstly, Geikie Gorge is a relatively stable environment that contains large quantities of water throughout the year. Thus, seasonal differences in its productivity (as noted in the preceding section) will be less than in tributaries and small pools of the catchment. Secondly, three species are apparently obligate piscivores (*C. leucas, L. calcarifer* and *P. pristis*) and one species is a specialised detrital feeder (*N. erebi*). If these species are not considered during pairwise comparisons of dietary overlap, the proportions of fishes with similar diets changes considerably. During the wet season, for example, there was no discernable difference in ~42% of the pairwise comparisons, which reduced to ~25% in the early dry and increased back to ~40% in the late dry. Thus, if species that are highly specialised for a particular diet, i.e. those that are less likely to be able to readily change their diets in response to changes in food availability, are removed from analysis, comparisons of those species that can respond strongly support this hypothesis.

Contention remains as to whether dietary (and resource) overlap of freshwater fish communities is highest or lowest in periods of low production, such as the tropical late dry season (Schoener 1974). Some argue, for example, that dietary overlap decreases in periods of low production in support of the 'competitive exclusion principle' (Zaret & Rand 1971; Angermeier & Karr 1983; Pusey & Bradshaw 1996). Alternatively, other studies indicate that dietary overlap increases when habitat and food resources become limited (Arthington 1992), and thus predators become less selective (Blaber 1986). The current study in some ways supports both theories, as the types and amount of foods present and the inclusion or exclusion of specialist feeders in analyses has a significant bearing upon the interpretation of data. The apparent contradiction of these two views can be resolved by considering the magnitude of the reduction in food availability. Thus when food is abundant, the probability of encountering many foods types is high, the return for capture/handling of many of these food types, even if they are of low calorific value, is likely to provide a net positive gain in energy. If a food type's density becomes reduced below a certain point, organisms will maximise energy returns by selecting foods to which they are particularly well adapted to capturing/processing. If food becomes even less abundant, organisms may have no choice other than the consumption of whatever food they can find/catch/process, in order to survive. When considering resource overlap and/or resource partitioning, it is therefore vitally important to consider how limiting the resource may be.

$\delta^{13}C$ and $\delta^{15}N$ values also suggest that dietary overlap was highest in the wet season, lowest in the early dry and increased again in the late dry season. For example, the distribution of $\delta^{13}C$ vs $\delta^{15}N$ values of the fishes in the wet season is contracted, indicating similarities in the food items assimilated. In the early dry season data points are expanded, whereas in the late dry season these points are again compressed. A 'compression' of food web structure was also observed during the Ord River isotope study by Trayler *et al.* (2003). In that study, the food web structure present in September (comparable to the late dry season in this study) was compressed in comparison to that observed in June (comparable to the early dry season in this study).

CONCLUSIONS

The use of $\delta^{13}C$ and $\delta^{15}N$ isotope and stomach content analysis indicated that differences often exist between the food types consumed and those that are energetically important to a species. For example, while this study supported the finding that omnivory is prevalent in the Fitzroy River, it strongly suggests that filamentous algae and other plant sources may not be as important in the diet as first suspected. Stable isotope analysis also indicated that prey types that persist throughout the year, including fish, molluscs and *M. spinipes*, may in fact be more important sources of the energy than dietary data revealed. This study also supports the view that juvenile fishes target high energy food items. Finally this study supports the notion that many species will maximise their energy intake in response to changes in resource availability.

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The Functional Habitat Concept does apply to fish assemblages of the regulated Lower Ord River, Western Australia

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This paper tests the applicability of the Functional Habitat Concept (FHC) to the fish fauna of the regulated Lower Ord River (LOR), a highly regulated lowland tropical river in the remote Northern Province of the Kimberley region of Western Australia. The underlying tenet of the FHC is that in-stream hydrological and physical processes form distinct habitats, and where these habitats support distinct faunal assemblages they are considered 'functional' habitats. Eight 'potential' in-stream habitats were identified in the LOR on the basis of their physical properties across wet and dry seasons. Multivariate and species preference analysis of fish data indicated deep and shallow water habitats supported distinct fish assemblages. Shallow water habitats were characterised by small-bodied species and juveniles of large bodied species, while deep water habitats supported adults of smaller species and large-bodied fishes. Four 'functional' habitats were identified in the dry season (shallow backwaters, gravel-cobble runs, flooded riparian vegetation and channel pools). Most (except channel pools) were also discernable in the wet season, together with emergent macrophyte habitat. Individual species and life stages demonstrated clear habitat preferences, with shallow water habitats supporting greater species richness than deep water habitats. Between habitat differences were greatest in the dry season, as was the number of species with significant preferences to specific habitats. Given the importance of shallow water habitats, and their susceptibility to impacts from further abstraction, environmental flows for the LOR must be designed to protect and maintain the current distribution and area of these key habitat types to maintain their dependent faunas. In a region where the fauna has been little studied, the FHC potentially aids in the preservation of fish diversity as it identifies critical functional habitats for managers to maintain.

KEYWORDS: Kimberley, environmental flows, river management, tropical river

INTRODUCTION

Rivers in the remote north of Australia are relatively free from the pressures of development affecting those in the south of the continent (*i.e.* impoundment, regulation, abstraction and diversion) (WRC 1997). However, Australia is experiencing a drying climate (Kirono *et al.* 2011), and there is mounting pressure to develop these rivers, particularly for irrigated agriculture (Storey & Trayler 2006). The tyranny of distance from major population centres also means that these northern Australian systems have been seldom studied, with relatively little known of their ecologies compared with their counterparts in more southern climes. As a result, river managers have a poor knowledge base on which to make decisions, such as determining environmental flows (Trayler *et al.* 2002; Storey & Trayler 2006; Arthington *et al.* 2006). Gathering the necessary ecological information can be a time consuming exercise, and in the face of pressing development, an alternative approach is required. Working at the habitat level may be such an approach.

The process of dividing streams into habitat types is widely used in restoration ecology, biological monitoring and fishery management, and this practice is based on the acceptance of the assumption that habitats have some consistent ecological meaning, and working at the habitat level will "make [the system] easier to study, understand or manage" (Rabeni *et al.* 2002). The acceptance of the linkage between species richness and habitat diversity is well entrenched in theoretical ecology (see Rabeni *et al.* 2002 and references therein), to the point where habitat is used as a surrogate for diversity; with management of habitats being the pragmatic goal. Therefore, habitats are proving useful for river survey, management and rehabilitation, as they provide a rapid and effective source of information of sufficient detail to assess the ecosystem without the need for painstaking identification of fauna or complex hydraulic modelling (Kemp *et al.* 2000).

As noted by Kemp *et al.* (2000), biological communities of rivers have been well studied over many years by ecologists, as have the processes and dynamics of channel morphology and hydraulics by hydrologists and geomorphologists. But, it is only in recent years that these parallel fields in stream ecology and geomorphology have been linked, especially in relation to habitats (Buffagni *et al.* 2000; Sullivan *et al.* 2004; Vezza *et al.* 2012).

The importance of habitats in fish ecology is well documented and has influenced the development of approaches for rapid bioassessment of river health using fish (Kennard *et al.* 2006; Parasiewicz 2007a, b). Very strong relationships have been reported between fish and habitat diversity (Joy & Death 2003; Pratt & Smokorowski 2003; Kennard *et al.* 2006; Rayner *et al.* 2008; Troia & Gido 2013). Water depth, velocity, substrate composition and cover have all been reported as key variables influencing fish diversity, with decreases in diversity occurring in association with reduced habitat diversity (Jowett & Richardson 1995; Smith & Kraft 2005; Stefferud *et al.* 2011). Essentially, different species of fish occupy different spatial units, with separation occurring vertically based on morphology, ontogeny and feeding habit (Moyle & Vondracek 1985; Gozlan *et al.* 1998; Jackson *et al.* 2001). In regulated rivers, habitat relationships have historically been used in the determination of environmental flows by calculating 'habitat suitability curves' for individual species (Capra *et al.* 1995; Jowett & Richardson 1995; Stewart *et al.* 2005). This approach has been useful for managing systems for single species, but requires detailed autecological information and is therefore prohibitive for systems supporting high species diversity.

One of the products of the collaboration between ecologists and hydrologists has been the Functional Habitat Concept (FHC), which grew out of the known association between the quality of in-stream habitats and the diversity of species they support (Harper & Everard 1998; Newson & Newson 2000). The concept was principally developed for managing macroinvertebrate assemblages, and is based on the assumption that conserving habitats ultimately conserves biodiversity (Tickner *et al.* 2000; Rabeni *et al.* 2002). As summarised by Buffagni *et al.* (2000), habitats that are recognisable from simple visual survey are termed 'potential habitats'. Where the numerical analysis of the faunal assemblages of these habitats produces an objective classification of habitats which support different assemblages, these are then regarded as 'functional habitats'. Although their definition is based in structural aspects of the fauna, the term functional habitats recognises how important the presence or absence of the various functional habitats might be for river processes, ecological 'health' and diversity of biota (Buffagni *et al.* 2000).

The FHC is based on the premise that it is possible to manage habitats in rivers far more easily than it is to manage species (Armitage & Pardo 1995; Buffagni *et al.* 2000; Kemp *et al.* 2000; Tickner *et al.* 2000), particularly in species-rich systems, and those where little is known of the life history or ecological requirements of individual species (Armitage & Pardo 1995). Since its development, the FHC has gained acceptance and has been widely employed in the Northern Hemisphere, i) to more clearly detect the effects of lowland river regulation in preference to more conventional biological assessment techniques (Armitage & Pardo 1995), ii) as a basis to establish cost-effective monitoring programs for improved river management (Buffagni *et al.* 2000; Troia & Gido 2013), iii) to maximise habitat heterogeneity and therefore biodiversity in river rehabilitation projects (Moulton *et al.* 2007; Suen & Su 2010), and iv) in the assessment of the impact of flow reduction on lotic fauna (Brunke *et al.* 2001; Vezza *et al.* 2012). Because river habitats are influenced by geomorphological processes (Harper & Everard 1998), they are sensitive to anthropogenic disturbance, such as flow regulation, and thus are an important focus for river management (Armitage *et al.* 2001). Indeed, from a management perspective, flow-related changes in habitat distribution and extent are more easily discerned than changes in the distribution, abundance and biomass of species based on infrequent sampling of populations. If flow volume, duration and frequency are sufficient to conserve diversity of in-stream habitats, then the corollary is that aquatic biodiversity also will be protected.

The FHC has been mainly tested on macroinvertebrate assemblages of European rivers (Armitage & Pardo 1995; Buffagni *et al.* 2000; Kemp *et al.* 2000; Brunke *et al.* 2001), with few instances of it being applied to fish assemblages (Copp 1991; Harper & Everard 1998; Kemp *et al.* 1999; Carl 2000; Crook *et al.* 2001). Prior to its application to the Ord River (Storey & Lynas 2007), the FHC had not been applied in Australia, although habitat associations have been studied (see Boys & Thoms 2006; Kennard *et al.* 2006; Rayner *et al.* 2008). The efficacy of this tool in river management in Australia will largely depend on the presence of discrete, easily recognisable physical habitats that support distinct suites of species (*sensu* functional habitats; Armitage & Pardo 1995; Pardo & Armitage 1997; Kemp *et al.* 1999, 2000; Buffagni *et al.* 2000; White & Irvine 2003).

The Ord River, in the remote north of Western Australia presented an opportunity to trial the FHC. Currently, approximately 90% of the catchment area is impounded to provide water for irrigated agriculture and for the generation of hydroelectric power. There are plans to more than double the area under irrigation, which could triple water demand. If this increased demand were to be met, it would mean a reduction in the amount of water for the environment (Storey & Trayler 2006). The State agency responsible for river management was tasked with developing an environmental flow for the river, but with little understanding of its ecology (Trayler *et al.* 2002; Storey & Trayler 2006). Preliminary surveys revealed a diverse macroinvertebrate and fish fauna, with many undescribed macroinvertebrate species, and a paucity of ecological or life history information for fish and macroinvertebrates (Storey & Trayler 2006). Therefore, the FHC was seen as a means to manage this system. The aim of this study was to test whether the underlying tenets of the FHC apply to fish assemblages of the LOR, namely: 1) do easily recognisable habitats exist within the system?; 2) do they support distinct fish assemblages?

This is the second of two studies on the application of the FHC to management of the Ord River, the first demonstrating concordance between macroinvertebrate fauna and habitat types (Storey & Lynas 2007).

METHODS

Study Area

The Ord River, located in the Northern Province (Unmack 2013) of the Kimberley region of Western Australia (Figure 1), is one of the state's major river systems, around 650 km long, with a catchment area of 46,100 km^2. The climate is semi-arid to arid monsoonal with two distinct seasons: a warm, dry season (May to October) and a hot, wet season (November to April). Monsoonal depressions and tropical cyclones are responsible for the vast majority of annual rainfall (ca. 870 mm per annum at Kununurra), with 90% falling during the wet season (Trayler *et al.* 2002).

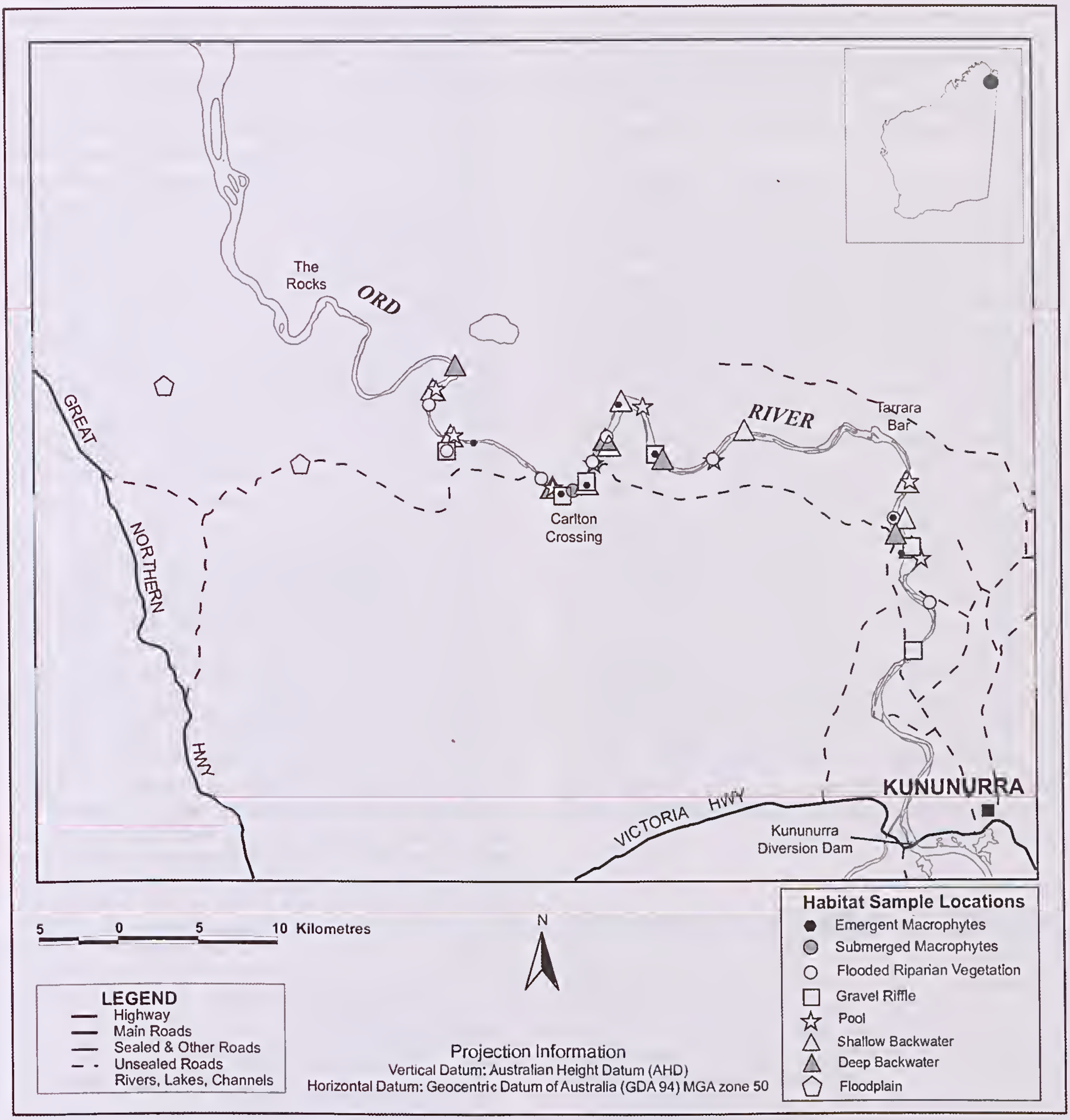


Figure 1 Location of habitats sampled on the Lower Ord River, Western Australia.

The Ord River is impounded by the 13.7 m high Kununurra Diversion Dam (KDD), which forms Lake Kununurra, and the 98.5 m high Ord River Dam (ORD) a further 55 km upstream, which forms the much larger Lake Argyle (surface area 74 000 ha, storage 10 700 GL). Water is released via the ORD into Lake Kununurra to provide a hydraulic head to feed water to irrigation paddocks. Water is then released from the KDD to maintain flows in the river downstream of the dams; the Lower Ord River (LOR). Regulation has transformed the system from a seasonally-flowing to a permanently-flowing river. Wet season peak flows are much reduced, but there is now constant flow during the dry season. As a result the system supports a greater abundance of fish, birds and crocodiles than would historically have been present (Storey & Trayler 2006). Small but important recreational and commercial fisheries have developed subsequent to regulation, as has the listing of two Ramsar wetlands of international importance. The greatest effect of increased irrigation will be a decrease in mean dry season flows, from the current ca. 80 m^3 sec^{-1} to ca. 40–45 m^3 sec^{-1}. This will result in an approximate 50 cm drop in current late dry season water levels. Modelling indicates that reduced discharge is likely to change the proportion of shallow to deep water habitats in the low-flow dry season, particularly the area of habitats along margins and shallows, as well as the rapids/gravel runs. However, there will be little effect on current wet season flows which are determined by high intensity monsoonal and cyclonic rains and the seasonally flowing, but unregulated Dunham River which enters the LOR below the KDD, providing wet season high flows (Trayler *et al.* 2002).

Sampling in the current study was conducted along the LOR, a meandering 70 km lowland section between the KDD and the Ord River estuary. The dry season channel is approximately 150 m wide with pools up to 5 m deep. Approximately 80% of the LOR consists of long pools (each 2–3 km in length), interspersed by rock bar/boulder rapids and gravel/cobble runs. These large pools are lined by a diversity of habitats, including shallow submerged macrophyte beds (predominantly *Vallisnaria americana* Michaux), beds of emergent reeds/rushes (*Phragmites australis* (Cav) Trin. Ex Steud, *Typha domingensis* Pers) adjacent to deeper banks, shallow backwaters, and shorelines of sand and silt. Riparian vegetation along the shoreline consists of a mixture of silver cadjeput, *Melaleuca argentea* W. Fitz., cadjeput *Melaleuca leucadendra* (L.) L., river gum *Eucalyptus camaldulensis* Denh, freshwater mangroves *Barringtonia angulata* (L.) Gaertn., white dragon tree *Sesbania formosa* F. Muell., and pandanus palms *Pandanus aquaticus* R. Br (Doupé & Pettit 2002). The river supports regionally diverse fish (~ 30 species) and macroinvertebrate (~ 170 species) faunas (Storey & Trayler 2006), and waterbird fauna (115 species of resident and migratory waterbirds and shorebirds) (Burbidge *et al.* 1991; Halse *et al.* 1996). It also supports large populations of the predominantly piscivorous freshwater crocodile *Crocodilus johnstoni* Krefft, but also the aggressive, potentially human-eating estuarine species *Crocodilus porosus* Schneider. Both species are protected.

Field sampling

Sampling was conducted in the late dry season (16th–26th October 2001), when conditions were hot (39–43 °C) and humid, with occasional isolated thunderstorms. Sampling was then repeated in the late wet season (15th–24th April 2002), when seasonal rains had finished and air temperatures were approximately 35 °C, but river levels were still elevated. Although not gauged, discharge on each sampling occasion was constant over the sampling period, with depth changing < 10 cm. To minimise spatial bias, the LOR was divided into lower (Carlton Crossing to The Rocks), middle (Tarrara Bar to Carlton Crossing) and upper (KDD to Tarrara Bar) reaches and replicate samples of each habitat stratified across all three reaches in each season (Figure 1). Logistical constraints such as daily travel time by boat from field camps, and limited boat access to some reaches due to impassable rapids and no road access, meant that sampling sites were not evenly distributed along the length of the reach. Due to the high risk of attack from estuarine crocodiles, sampling was conducted predominantly from a boat.

Eight visually discernible 'potential' habitat types were identified, grouped into two broad categories: i) deep water habitats (≥ 1 m); deep backwaters, river pools, deep water adjacent to stands of emergent macrophyte (*Phragmites australis*), and flooded riparian vegetation along the margins and on low benches, and ii) shallow water habitats (< 1 m); shallow backwaters, submerged macrophyte beds, gravel-cobble runs and floodplain lagoons. To test whether these visually identifiable habitats represented discrete habitat types, a range of environmental variables were measured at each replicate site (Table 1). Physico-chemical variables were measured *in situ* using a Yeo-Kal Model 611 multiprobe water quality analyser. Water velocity was measured with a Marsh-McBirney velocity meter at approximately 0.6 of water depth. Water depth was measured at 10 randomly selected locations within each site with a graduated staff (< 1.5 m) or a Garmin Model 135 GPSMAP sounder (> 1.5 m), and location of sites recorded with the Garmin GPS. Percent cover of different substrate and vegetation types were estimated visually (where water clarity allowed), or estimated by 'sounding' the bottom with a plumb line. To limit variation due to different observers, all estimations were made by the same sampler. As an indication of habitat heterogeneity, the number of organic and inorganic substrate types represented at each site was totalled.

To test whether these 'potential' habitats supported distinct fish assemblages, fish were sampled from each replicate habitat using two standard methods. These methods have been employed extensively throughout the Northern Province (Bishop *et al.* 1986, 1990; Larson 1999, WRC 2003; Storey unpub. data) to provide as representative sample as possible of communities in deep and shallow water habitats. All deep water habitats (pools, deep backwaters, emergent macrophyte beds and flooded riparian vegetation) were sampled using multi-panel gill nets (30 m long, consisting of six panels, each 5 m in length with a 2 m drop and stretched mesh size increasing in ~ 2.5 cm increments from 2.5 to 15 cm). For each replicate sample, two gill nets were set for 3 h (either from 0800 to 1100 h, or from 1400 to 1700 h). Nets were set 50 m apart, angled at 30–45 degrees to the bank (depending upon strength of flow), with smallest mesh size attached to the bank. In addition, two replicate longlines (20 m long, with 12 hooks on each line (Mustad Tuna Circle size 11/0 on 30 kg traces), baited with fresh fish) were set for the same period as the gill nets. Nets and lines were recovered at the end of the set period and all fish removed and catch by both methods combined. Gill nets were not effective in sampling shallow water habitats, therefore, a beach seine (20 m long x 1.5 m deep) constructed from 10 mm diamond mesh was used. It was not possible to conduct seine netting in deep water habitats. Seining at shallow water habitats was standardised either by drawing the seine through the whole habitat (i.e. small, shallow backwaters), or by walking the seine perpendicular to the shore and encircling a set area of habitat. Samplers carried a tape measure and paced the distance thereby sampling 20 m^2 of each habitat. Longlines were also set in each shallow water habitat, as per above. Longlines were recovered at the end of the set period and catch by both methods combined. All fish caught were identified to species, principally following the taxonomy of Allen (1989) and Allen *et al.* (2002), weighed and fork length (FL; snout to fork of tail or snout to posterior margin of tail if the caudal fin was not forked) recorded before being released. Where large numbers of small species were taken, a random sub-sample of at least 10 specimens

Table 1 Measured and derived environmental variables.

Variable	Code
Temperature (°C)	temp
pH (H^+)	pH
Dissolved oxygen (% saturation)	DO%
Dissolved oxygen (mg L^{-1})	DO mg/L
Conductivity (mS cm^{-1})	EC
Salinity (mg L^{-1})	sal
Turbidity (NTU	turb
Redox potential (mV)	redox
Velocity (cms sec^{-1})	vel
Mean depth (cm)	depM
Variance in depth (cm)	depV
Mineral substrates (total % cover within habitat)[1]	min
Bedrock (% cover)	bedr
Boulders >256 mm (% cover)	boul
Cobbles 64–256 mm (% cover)	cobb
Pebbles 16–64 mm (% cover)	pebb
Gravel 4–16 mm (% cover)	grav
Sand 1–4 mm (% cover)	sand
Silt <1 mm (% cover)	silt
Emergent macrophyte (% cover within habitat)	emerg
Submerged macrophyte (% cover within habitat)	submerg
Floating macrophyte (% cover within habitat)	float
Algae (% cover within habitat)	algae
Detritus (% cover within habitat)	detr
Riparian vegetation (% cover within habitat)	ripvegco
Large woody debris (>10 cm diameter) (% cover within habitat)	LWD
Root mats (% cover within habitat)	rootm
Riparian vegetation (% cover within habitat)	ripveg
Snag (<10 cm diameter) density (1–3; 1 = sparse, 3 = dense)	snag
Habitat complexity (total number of substrate types present)	complx
Bank angle (degree)	bkang
Undercuts (% cover within habitat)	underc
Substrate compaction (1 = loose array, 5 = armoured, tightly packed)	compct

[1] Mineral substrates and substrate surface areas were estimated visually in shallow water or by 'sounding' the bottom with a lead weight in deeper water.

were individually weighed and measured and the remainder counted and a total weight recorded.

Where present, two replicates of each habitat were sampled within each reach during each season, providing a maximum of six replicates per habitat in any season. During the late wet season, water levels in the main channel were at least 3 m higher than during the late dry season. As a result, the distribution of habitats changed and not all habitats were present in both seasons. In the dry season, lower water levels meant that floodplain habitats were dry, deep backwaters did not exist, and flooded riparian zones were restricted to a narrow margin along the shore. In the wet season, higher water levels meant that shallow backwaters became deep backwaters, the floodplain was inundated and so could be sampled, and broad, low benches vegetated with silver cadjeput, cadjeput, freshwater mangroves, white dragon tree and pandanus became broad areas of flooded riparian habitat. Gravel-cobble runs and submerged macrophyte beds were not accessible due to deep, turbid water over these habitats in the wet season. Though there was some seasonal tidal influence in the most downstream part of the study area (The Rocks), all reaches surveyed were freshwater.

Data analysis

Amongst habitat differences in environmental variables and fish species richness were investigated by two-way ANOVA, by habitat and season (IBM SPSS Statistics v19). The potential confounding influence of different sampling methods is here acknowledged, particularly how abundance of fish caught may bias the number of species collected (Gotelli & Colwell, 2001). Therefore, species richness data were re-estimated using rarefaction, performed using PRIMER (v6) software package (Clarke & Gorley 2006). The assumptions of normality and homogeneity of sample variances were checked using Shapiro-Wilk (Shapiro & Wilk 1965) and Levene's (Levene 1960) tests, respectively. Environmental data were $\log_{10}(x+1)$ transformed or arcsine transformed (percent data), where appropriate. Where multiple tests on environmental variables were performed, a

Bonferroni correction was applied to minimise the chance of Type I errors, whereby critical $p = (0.05/n)$, where n = number of tests performed. Tukey's HSD multiple range test was used to locate between-habitat differences where there was a significant main effect.

Multivariate patterns in environmental and fish presence/absence data were analysed using procedures from the PRIMER (v6) software package (Clarke & Gorley 2006). The permutational multivariate analysis of variance (PERMANOVA) add-on to PRIMER v6 was used to test for significant ($p < 0.05$) habitat effects on environmental variables or fish species assemblages (Anderson 2001a, b; McArdle & Anderson 2001; Anderson *et al.* 2008). Non-metric Multi-Dimensional Scaling (nMDS) ordination plots (Clarke & Warwick 2001) were constructed to visualise differences between habitats. nMDS ordinations were based on Euclidean distance measures for environmental data, and Bray-Curtis similarity measures for fish presence/absence data. Ordinations were depicted as two-dimensional plots.

In recognition that different life stages within a species, particularly for fish, have different habitat requirements (Harris & Kangas 1988; Cowx & Welcomme 1998), prior to analysis species were divided into 'pseudospecies' based on size classes. A maximum of three size classes were recognised per species, corresponding approximately to juveniles, sub-adults and adults as determined from the literature (Allen 1982; Bishop *et al.* 2001; Allen *et al.* 2002). Analyses were performed to test between individual habitat types and between deep and shallow water habitats.

Habitat preferences of pseudospecies were examined using both chi-squared (χ^2) tests and the similarity percentage analysis (SIMPER) within PRIMER, both of which assess species occurrences across habitats. The χ^2 test was applied only to those pseudospecies with sufficient levels of occurrence within and across habitats to allow valid analysis, as determined by the statistical package. Analyses were significant if $p < 0.05$, and within a pseudospecies, habitats with the greatest deviation of the observed from the expected frequency were taken to indicate a preference of the pseudospecies for that habitat type.

Distance-based linear models (DISTLM) were used to explore multivariate relationships between environmental variables (Table 1) and assemblage data using pseudospecies (Anderson 2001a, 2002; McArdle & Anderson 2001). The final multivariate multiple regression model that best explained the variation in the species data was chosen using the stepwise forward-selection procedure and AIC selection criterion. Significance of regression relationships was assessed using 9999 random permutations of the data.

RESULTS

Environmental descriptors of habitats

Significant between-habitat and -season differences were detected for 15 and 5 of the environmental variables, respectively (ANOVA, Table 2). Most measures of water quality showed little spatial variability, indicating waters were well mixed both vertically and laterally across all habitat types. The exceptions were lower pH and higher temperature in floodplain habitat, resultant of shallow, standing waters and soils rich in organics. Significant spatial differences were identified for velocity, depth, bank angle, habitat complexity (e.g. % mineral substrate, pebbles, silt, snags), and vegetation cover (e.g. emergent/ submerged/floating macrophytes, algae, root mats and trailing riparian vegetation). Many of these habitat differences reflected the readily observed physical

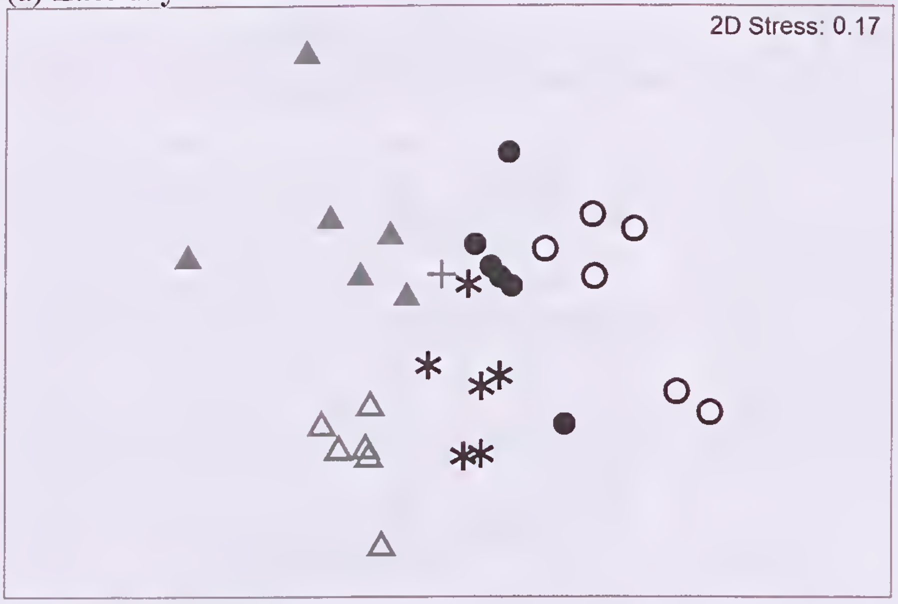
Table 2 Results from two-way ANOVA and Tukey's *post hoc* test on environmental variables measured over two seasons (W = late wet; D = late dry) across eight habitat types (B = shallow backwater; DB = deep backwater; E = emergent macrophyte; F = flooded riparian vegetation; FP = floodplain; G = gravel-cobble run; P = pool; SM = submerged macrophyte). Only variables for which there was at least one significant main effect are shown here (p <0.05). Habitats or seasons joined by a common line are not significantly different (Bonferroni adjusted p value <0.002). Arithmetic means (+ 1 SE in parentheses) are presented for each habitat/season.

Habitat variable	Habitat (df =7)		Season (df =1)		Interaction (df =3)		Pairwise comparison									
	F	*p*	F	*p*	F	*p*	Habitat (Tukey's HSD multiple comparison test)								Season	
pH	3.40	0.00	22.10	<0.0001	0.69	>0.05	DB	P	F	E	SM	B	G	FP	W	D
							8.5	8.3	8.1	8.1	8.0	8.0	7.7	6.9	8.2	7.8
							(0.19)	(0.18)	(0.14)	(0.19)	(0)	(0.20)	(0.24)	(0.26)	(0.19)	(0.18)
Turbidity	1.63	>0.05	21.58	<0.0001	0.87	>0.05	SM	B	G	F	E	P	FP	DB	D	W
							20.7	14.6	15.6	14.9	14.3	12.8	10.6	9.8	17.9	11.4
							(0)	(1.82)	(2.34)	(1.63)	(1.68)	(1.32)	(5.55)	(0.66)	(1.92)	(1.97)
Temp	2.60	0.0231	0.08	>0.05	0.22	>0.05	FP	SM	DB	E	B	P	F	G	W	D
							33.1	30.7	30.6	30.4	30.3	30.1	30.1	30.0	30.7	30.3
							(2.12)	(0)	(0.23)	(0.27)	(0.51)	(0.32)	(0.27)	(0.39)	(0.58)	(0.40)
Velocity	15.04	<0.0001	1.23	>0.05	3.78	0.0162	G	E	P	F	DB	SM	B	FP	D	W
							56.1	26.9	25.2	9.4	7.8	3.0	0	0	18.8	12.9
							(0.20)	(4.90)	(5.45)	(2.95)	(4.50)	(0)	(0)	(0)	(5.14)	(2.60)

Table 2 (cont.)

Habitat variable	Habitat (df =7)		Season (df =1)		Interaction (df =3)		Pairwise comparison									
							Habitat (Tukey's HSD multiple comparison test)								Season	
	F	*p*	F	*p*	F	*p*										
Depth	24.61	<0.0001	0.01	>0.05	15.39	<0.0001	P 3.6 (0.29)	E 2.4 (0.38)	DB 2.2 (0.28)	F 2.2 (0.29)	SM 0.9 (0)	B 0.5 (0.08)	G 0.5 (0.08)	FP 0.4 (0.16)	D 1.7 (1.24)	W 1.9 (1.22)
%Pebble	25.14	<0.0001	3.65	>0.05	1.91	>0.05	G 63.3 (5.70)	E 7.1 (3.45)	F 4.8 (2.85)	P 4.7 (4.65)	B 0.2 (0.15)	FP 0 (0)	DB 0 (0)	SM 0 (0)	D 15.1 (4.38)	W 1.0 (1.0)
%Sand	2.44	0.0313	1.34	>0.05	0.64	>0.05	B 41.5 (13.30)	E 40.4 (6.60)	P 36.0 (14.35)	F 17.9 (10.95)	DB 11.7 (0.0)	G 6.2 (0.80)	FP 0 (0)	SM 0 (0)	W 24.1 (5.71)	D 23.5 (6.58)
%Silt	4.90	0.0003	3.81	>0.05	2.58	>0.05	FP 100 (0)	SM 100 (0)	DB 88.3 (8.30)	F 68.4 (13.75)	B 56.4 (13.90)	P 45.0 (15.65)	E 28.8 (3.30)	G 0.5 (0.50)	W 70.0 (7.75)	D 44.3 (11.10)
%Mineral	14.53	<0.0001	0.78	>0.05	1.70	>0.05	G 100 (0)	P 78.0 (9.55)	DB 77.2 (5.60)	B 76.8 (10.60)	E 38.6 (4.70)	F 34.7 (6.50)	SM 18.0 (0)	FP 4.0 (4.0)	D 59.3 (4.54)	W 49.8 (8.27)
%Emergent veg.	61.81	<0.0001	0.91	>0.05	2.05	>0.05	E 56.3 (2.70)	FP 30.0 (30.0)	DB 4.2 (2.0)	B 2.1 (1.70)	F 1.7 (1.25)	P 0.5 (0.50)	G 0 (0)	SM 0 (0)	W 15.0 (6.07)	D 10.8 (1.58)
%Sub-merged veg.	11.74	<0.0001	0.38	>0.05	0.39	>0.05	SM 75.0 (0)	FP 50.0 (40.0)	B 10.1 (6.75)	DB 0.8 (0.80)	E 0 (0)	G 0 (0)	F 0 (0)	P 0 (0)	D 13.5 (0.98)	W 10.8 (8.23)
%Floating	58.79	<0.0001	0.00	>0.05	0.00	>0.05	FP 15 (5.0)	B 0 (0)	E 0 (0)	DB 0 (0)	G 0 (0)	P 0 (0)	F 0 (0)	SM 0 (0)	W 2.5 (0.83)	D 0 (0)
%Algal cover	6.53	<0.0001	0.00	>0.05	0.00	>0.05	FP 0.5 (0.5)	B 0 (0)	E 0 (0)	DB 0 (0)	G 0 (0)	P 0 (0)	F 0 (0)	SM 0 (0)	W 0.1 (0.08)	D 0 (0)
%Detritus	3.09	0.0088	0.53	>0.05	1.13	>0.05	B 8.0 (3.30)	F 5.1 (1.40)	SM 5.0 (0.0)	DB 2.5 (1.10)	E 1.9 (1.15)	P 1.1 (0.40)	FP 0 (0.50)	G 0 (0)	W 3. (1.36)	D 2.6 (0.59)
%Trailing	5.18	0.0002	46.40	<0.0001	5.08	0.0038	D 5.8 (0.83)	F 4.0 (0.73)	P 2.3 (0.39)	B 1.4 (0.84)	E 0.6 (0.49)	FP 0 (0)	G 0 (0)	S 0 (0)	W 3.6 (0.87)	D 0.1 (0.10)
%Root mat	9.94	<0.0001	4.11	0.0480	1.12	>0.05	F 5.0 (0.75)	DB 3.7 (0.80)	P 3.4 (0.65)	E 0.5 (0.5)	B 0.1 (0.1)	FP 0 (0)	G 0 (0)	SM 0 (0)	W 2.4 (0.37)	D 1.1 (0.52)
%Riparian vege. cover	11.39	<0.0001	27.14	<0.0001	8.56	0.0001	F 42.1 (6.60)	DB 11.0 (2.90)	B 9.9 (5.90)	P 8.6 (3.35)	E 8.5 (4.45)	SM 5.0 (0)	FP 2.5 (2.50)	G 0.8 (0.80)	W 20.1 (5.75)	D 6.1 (2.46)
%Snags	16.88	<0.0001	0.78	>0.05	0.75	>0.05	F 2.1 (0.29)	P 1.2 (0.12)	DB 1.2 (0.31)	SM 1.0 (0)	E 0.7 (0.21)	B 0.2 (0.17)	G 0 (0)	FP 0 (0)	W 0.9 (0.20)	D 0.8 (0.14)
Habitat complexity	17.53	<0.0001	0.05	>0.05	0.46	>0.05	F 1.9 (0.22)	P 1.8 (0.19)	SM 1.0 (0)	DB 1.0 (0.26)	E 0.9 (0.33)	B 0.2 (0.17)	G 0 (0)	FP 0 (0)	W 1.0 (0.19)	D 1.0 (0.19)
Bank angle (degrees)	11.20	<0.0001	26.70	<0.0001	4.08	0.0115	P 58.4 (6.10)	DM 43.3 (10.1)	F 41.7 (5.55)	E 40.4 (10.25)	SM 35.0 (0)	B 17.1 (2.65)	G 11.7 (1.70)	FP 5.0 (0)	D 42.2 (4.12)	W 26.1 (6.72)

(a) Late dry season



(b) Late wet season

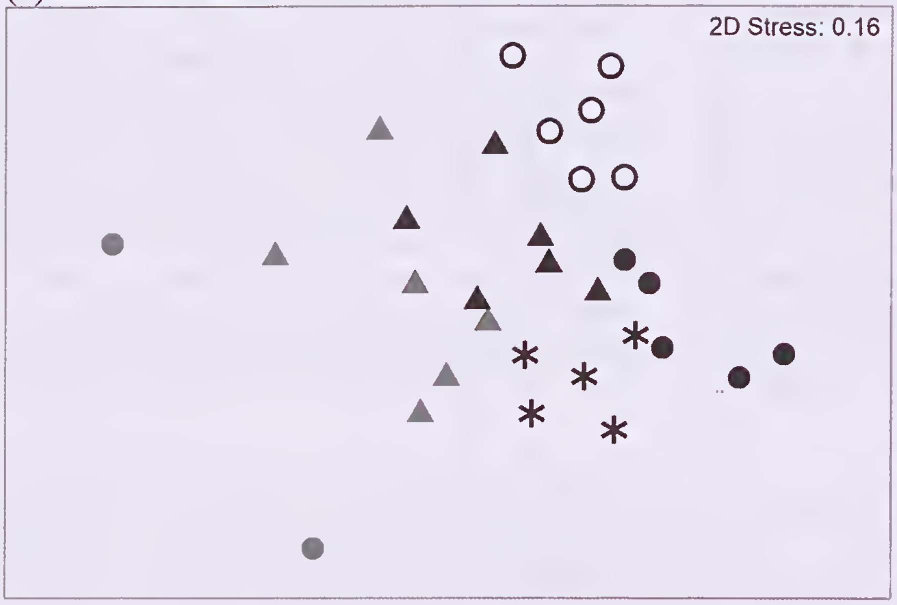


Figure 2 Unconstrained nMDS ordination plots, comparing environmental variables among habitats for each season on the basis of Euclidean distance measure.

differences that were used to visually define habitats. Interaction terms were significant for mean water depth and % riparian vegetation cover reflecting that changes in depth and cover were not consistent across habitats and between seasons (i.e. shallow backwaters moved laterally in the wet season to the edges of flooded benches which were well vegetated, therefore cover increased in the wet season, but depth stayed the same as in the dry season), but also that not all habitats were represented in each season. Seasonal differences reflected increasing depth and velocity during the wet season, with redistribution of habitats. For example, submerged macrophyte beds and gravel-cobble runs were drowned-out and therefore not accessible, previously shallow backwaters became deep backwaters, and new areas of shallow water appeared at the channel edge, often within or behind the margin of riparian vegetation.

There was a significant difference in environmental parameters between deep and shallow water habitats in both seasons as determined by PERMANOVA (Table 3). Within each season, pairwise comparison of each habitat type indicated significant separation of most habitats. In the dry season, habitats were significantly different from each other, with the exception of submerged macrophytes, which could not be differentiated from any other habitat owing to no replication of this habitat. Deep and shallow water habitats were the most distinctive in the dry as shown in the unconstrained ordination plots (nMDS, Figure 2a–b).

Fish assemblages within habitats

Sampling across all habitats in both seasons recorded 3 763 fish, representing 38 species from 28 families (Appendix). The majority of species were distributed throughout all three reaches of the LOR, with the exception of six species that are either 'marine or

Table 3 Results from (a) two-way PERMANOVA testing for season or habitat effects on the suite of environmental variables, based on Euclidean distance measure, and (b) pairwise comparisons for habitat effects within each season using permutations of the t-statistic. Significance level p(perm) <0.05; significant results for pairwise comparisons are indicated as, <0.05*, <0.01**. *NA* = not available; not all habitats were present in both seasons. Refer Table 2 for habitat codes.

(a) Main test	Habitat (df =7)				Season (df =1)				Interaction (df =3)			
	SS	MSS	F	p(perm)	SS	MS	F	p(perm)	SS	MS	F	p(perm)
Environmental variables	643	92	6.320	0.0001	130	130	8.928	0.0001	74	25	1.695	0.009

(b) Pairwise comparisons for habitat

	Late dry season					Late wet season				
	B	E	F	G	P	B	E	F	P	DB
E	2.223**					1.907**				
F	2.647**	2.267**				2.492**	3.136**			
G	2.884**	2.535**	3.237**			*NA*	*NA*	*NA*		
P	2.218**	2.155**	1.840**	3.272**		2.128	1.513**	2.518**		
SM	1.303	1.582	1.455	2.247	1.777	*NA*	*NA*	*NA*	*NA*	
DB	*NA*	*NA*	*NA*	*NA*	*NA*	1.669	1.882**	2.154**	1.453*	
FP	*NA*	*NA*	*NA*	*NA*	*NA*	1.480	2.042*	2.489**	2.120*	1.846*

Table 4 Results from two-way ANOVA and Tukey's *post hoc* testing for season (D = late dry; W = late wet) or habitat effects on fish species richness. Habitats or seasons joined by a common line are not significantly different (p value <0.05). Arithmetic means (+ 1 SE in parentheses) for species richness are presented for each habitat. Refer Table 2 for habitat codes.

Species variable	Habitat (df =7)		Season (df =1)		Interaction (df =3)		Pairwise comparison									
							Habitat (Tukey's HSD multiple comparison test)								Season	
	F	p	F	p	F	p										
Richness (no. of species)	2.73	0.023	0.01	0.987	3.83	0.015	SM	DB	F	B	P	E	FP	G	D	W
							7.53	6.3	6.2	5.8	5.8	5.3	4.5	2.9	5.7	5.2
							(0)	(0.70)	(0.49)	(0.49)	(0.65)	(0.52)	(1.2)	(0.70)	(0.34)	(0.31)

estuarine vagrants' or 'marine migrants' and which were only occasionally caught in the lower tidally-influenced reach, including *Elops hawaiensis* Regan, *Arrhamphus sclerolepis sclerolepis* Günther, *Sciades leptaspis* (Bleeker), *Marilyna meraukensis* (de Beaufort), *Thryssa* sp. and Mugilidae spp.

There were significant between-habitat differences in species richness, but no significant seasonal effect (Table 4). Fish species richness was ~ 60% less in gravel-cobble runs and floodplain habitats than in submerged macrophyte and shallow backwater habitats (Figure 3). This was primarily due to the presence of many juvenile and small-bodied fish species in these latter habitats.

Fish assemblages differed significantly between habitats (PERMANOVA, Table 5a). In the dry season, pairwise comparisons indicated the majority of habitats were significantly different with the exception of flooded riparian vegetation compared with emergent macrophyte beds and pools, and all comparisons with submerged macrophyte beds, reflecting small sample size of the latter (Table 5b). In the wet season most habitats were different from each other, except deep backwaters, pools and emergent macrophytes compared with each other (Table 5b). The nMDS ordinations on assemblages did not clearly distinguish individual habitats, but did show a general separation of shallow from deep water habitats in both seasons (Figure 4a–b).

SIMPER analyses revealed shallow water habitats to be characterised by small-bodied species (e.g. *Ambassis macleayi* (Castelnau), *Amniataba percoides* (Günther), *Glossogobius giuris* (Hamilton) and *Melanotaenia australis* (Castelnau)) and juveniles of large bodied species (*Liza alata* (Steindachner), *Lates calcarifer* (Bloch) and *Nematalosa erebi* (Günther)), while deep water habitats supported more adult and large-bodied fishes (e.g. *L. alata*, *Neoarius graeffei* (Kner & Steindachner), *Neoarius midgleyi* (Kailola & Pierce) and *N. erebi*). Faunal similarity within habitats was low, averaging 33% for deep water and 25% for shallow water habitats. Highest similarity amongst replicates occurred for flooded riparian habitat during

Table 5 Results from (a) two-way PERMANOVA testing for season or habitat effects on fish assemblages based on Bray-Curtis similarity measure, and (b) pairwise comparisons for habitat effects within each season using permutations of the t-statistic. Significance level *p*(perm) <0.05; significant results for pairwise comparisons are indicated as, <0.05*, <0.01**. *NA* = not available; not all habitats were present in both seasons. Refer Table 2 for habitat codes.

(a) Main test	Habitat (df =7)				Season (df =1)				Interaction (df =3)			
	SS	MSS	F	*p*(perm)	SS	MS	F	*p*(perm)	SS	MS	F	*p*(perm)
Richness (no. of species)	72258	10323	5.480	0.001	2445	2	1.300	0.23	8069	2690	1.428	0.111

(b) Pairwise comparisons for habitat

	Late dry season					Late wet season				
	B	E	F	G	P	B	E	F	P	DB
E	2.314**					2.892**				
F	3.148**	0.818				3.261**	1.048*			
G	1.617**	1.704**	2.172**			*NA*	*NA*	*NA*		
P	3.148**	1.100*	1.084	2.205**		2.628**	1.878	1.544*		
SM	1.135	1.224	1.930	0.946	2.072	*NA*	*NA*	*NA*	*NA*	
DB	*NA*	*NA*	*NA*	*NA*	*NA*	2.928**	1.067	0.888*	0.917	
FP	*NA*	*NA*	*NA*	*NA*	*NA*	1.641*	2.963*	3.598*	2.440*	2.940*

Table 6 Results of chi-square (χ^2) analysis of associations between eight habitats and 58 fish pseudospecies recorded from the LOR over two consecutive seasons. Only pseudospecies for which there was at least one significant association are shown. Values represent the percentage of samples from each habitats in which each species was recorded, with the number of samples given in parenthesis. Statistical significance of the χ^2 value is given as *p*. Percentage occurrences highlighted in **bold** indicate preferred habitat(s) of each pseudospecies. Codes for pseudospecies: L = adult, M = sub-adult, S = juvenile. Refer Table 2 for habitat codes.

	Late dry season							Late wet season						
Pseudospecies	B (6)	E (6)	F (6)	G (6)	P (6)	SM (1)	*p*	B (6)	DB (6)	E (5)	F (6)	FP (2)	P (5)	*p*
A. macleayi (L)	**33**	0	0	0	0	100	0.0076	33	0	0	17	50	0	ns
A. macleayi (M)	**17**	0	0	0	0	**100**	0.0041	67	0	0	0	**100**	0	0.0003
A. percoides (M)	**67**	0	0	**67**	0	100	0.0029	**100**	0	0	0	0	0	<0.0001
A. percoides (S)	**50**	0	0	0	0	0	0.0167	**67**	0	0	0	0	0	0.0014
N. graeffei (L)	0	67	**83**	33	**100**	100	0.0053	0	**100**	80	**100**	0	100	0.0004
N. graeffei (M)	0	50	**83**	17	**100**	0	0.0026	0	**83**	60	50	0	80	0.0466
N. midgleyi (M)	0	33	67	0	**83**	0	0.0077	0	17	20	33	0	20	ns
Ambassis sp. (M)	**33**	0	0	17	0	100	0.038	17	0	0	0	0	0	ns
C. ?stercusmuscarum	**17**	17	0	0	0	**100**	0.0357	17	0	0	0	0	0	ns
G. aprion	**17**	0	0	0	0	**100**	0.0041	33	0	0	0	0	0	ns
G. giuris	**100**	0	0	17	0	100	<0.0001	**67**	0	0	0	0	0	0.0014
H. compressa (L)	0	0	0	0	0	**100**	<0.0001	17	0	0	0	50	0	ns
H. jenkinsi	0	0	0	0	0	**100**	<0.0001	0	17	0	17	0	0	ns
L. alata (L)	67	50	**100**	0	**100**	0	0.0019	33	**83**	**100**	**100**	0	40	0.019
L. alata (M)	**83**	17	0	17	17	0	0.0184	17	67	20	17	0	0	ns
M. australis (L)	**50**	0	0	17	0	100	0.0173	**67**	0	0	0	**100**	0	0.0003
M. australis (S)	33	0	0	17	0	0	ns	17	0	0	0	**100**	0	0.0005
M. cyprinoides (S)	0	0	0	0	17	**100**	0.0041	17	17	20	0	0	0	ns
N. hyrtlii (L)	0	33	17	0	17	0	ns	0	33	20	**67**	0	0	0.042
N. erebi (L)	17	17	17	0	50	0	ns	0	**83**	80	83	0	40	0.0119
N. erebi (M)	17	33	17	0	**83**	100	0.0194	33	50	60	83	0	20	ns
N. erebi (S)	83	0	0	0	33	100	0.0014	67	33	20	17	0	40	ns
Plotosidae sp. 1	—	—	—	—	—	—	—	0	0	0	0	**100**	0	<0.0001
Plotosidae sp. 2	—	—	—	—	—	—	—	0	0	0	0	**50**	0	0.0085
P. gulliveri	33	0	0	0	0	100	0.0076	—	—	—	—	—	—	—
T. chatareus (L)	33	50	50	0	50	0	ns	17	**67**	0	83	0	20	0.0103

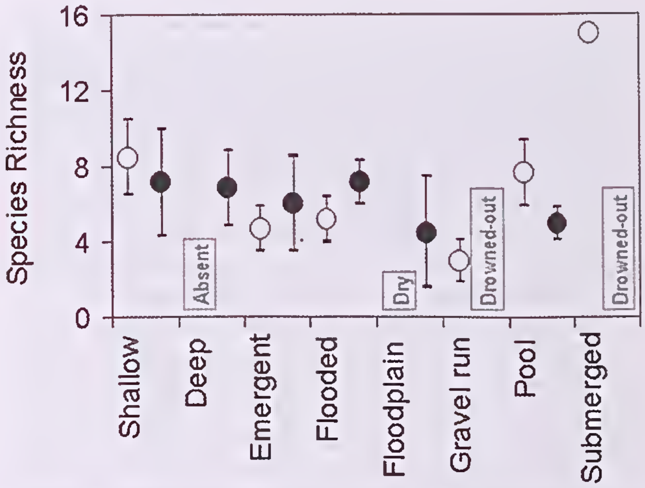
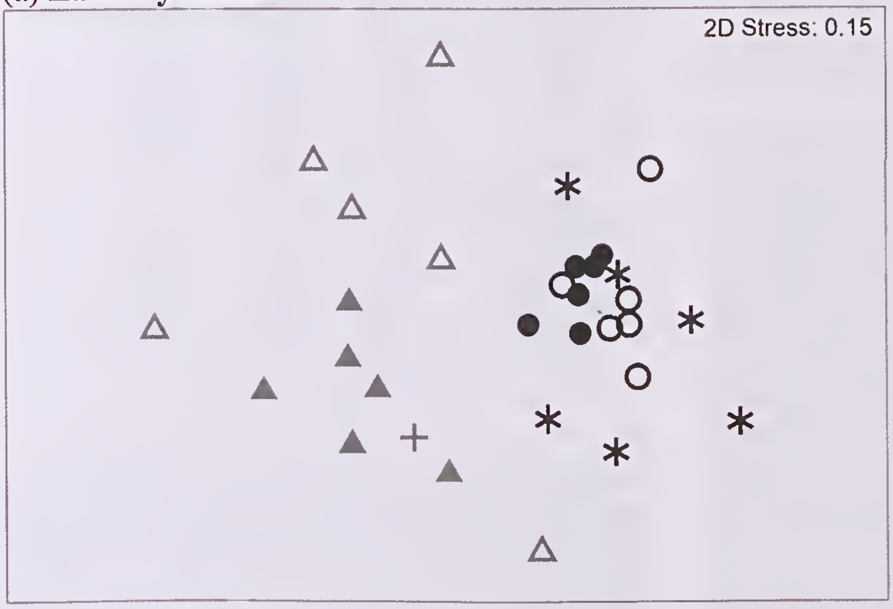


Figure 3 Mean (± 95% confidence interval) species richness of fish in each habitat in each season; ○ late dry, ● late wet.

the late wet (58%), whilst lowest similarity was within gravel-cobble runs (11%) during the dry.

Frequency analysis (χ^2, Table 6) indicated significant habitat preferences for 42% of pseudospecies present during the dry season and 27% of pseudospecies during the late wet. Of these, the majority favoured shallow backwaters during the dry, but had equal distribution amongst shallow and deep backwaters, floodplain, pool and flooded riparian habitat during the wet season (Figure 5). During the dry season, the shallow backwaters supported higher abundances of *Leiognathus equulus* and *Glossogobius giuris*. Sub-adult *Amniataba percoides* also displayed preference for shallow backwaters and gravel-cobble runs; they were the dominant fish in gravel-cobble runs during the late dry and in shallow backwaters during the late wet season. Floodplain habitat, which was only available during the wet season, was typified by *Ambassis macleayi* and *Melanotaenia australis*. In both seasons, the deeper water

(a) **Late dry season**



(b) **Late wet season**

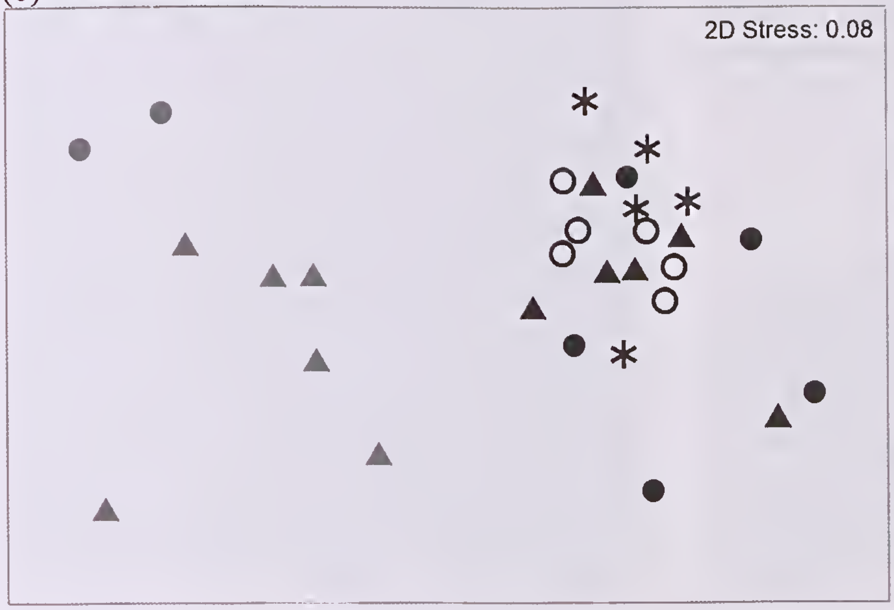


Figure 4 Unconstrained nMDS ordination plots comparing fish assemblages (presence/absence) among habitats for each season on the basis of Bray-Curtis similarity measure.

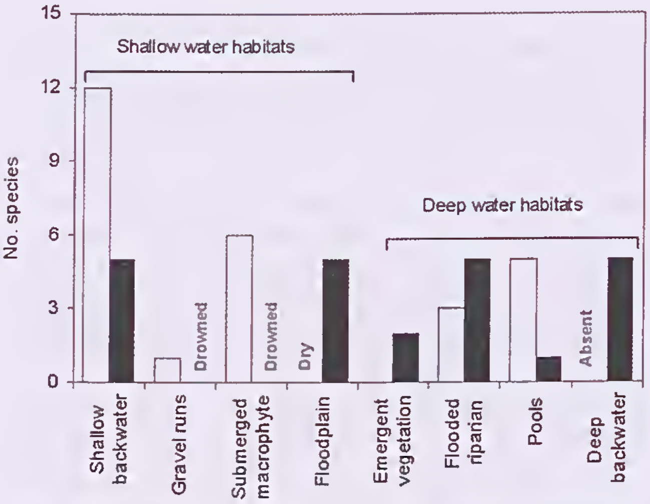


Figure 5 Number of fish life stages (pseudospecies) showing preferential habitat use in each season; □ late dry season, ■ late wet season, as determined by chi-square contingency table analysis.

habitats were characterised by adult *L. alata* and adult and sub-adult *N. graeffei*.

Multivariate multiple regression analysis identified five environmental variables with significant relationships with fish assemblages during the dry season (Table 7). The variable that individually explained the greatest amount of variation in species presence/absence data was bank angle (24.5%), followed by mean depth (21.9%), habitat complexity (17.2%), % snags (13.9%) and % pebble substrate (9.0%). Of these, stepwise forward selection showed that bank angle and % pebble were the best predictors, together explaining 32.3% of the total variation. In contrast to the dry season, analysis of wet season data identified nine significant environmental variables, three of which were also significant in the dry, i.e. habitat complexity, % snags and mean depth (Table 7). Individual variables that alone explained most variation in species presence/absence data in the wet were habitat complexity (18.2%), mean depth (17.9%), % snags (17.8%), % root mats (16.8%) and % submerged macrophyte (16.7%). The best predictor of species richness in the wet was a combination of four variables (Table 7) that collectively explained 39.4% of the total variation.

DISCUSSION

Evidence for the functional habitat concept

This study demonstrated that visually distinct 'potential' habitats within the LOR could be distinguished on the basis of their physical properties, and these habitats supported different fish assemblages, making them 'functional habitats' *sensu* Armitage & Pardo (1995), Kemp *et al.* (2000), Buffagni *et al.* (2000) and Tickner *et al.* (2000). Eight 'potential' habitats were identified by visual assessment, although not all habitats were present at all times due to seasonal changes in water levels. In the wet season, deep backwaters and floodplain habitats were present due to the higher water levels, but submerged macrophyte beds and gravel-cobble runs were not sampled because they were inundated by deep, fast flowing water and so were not accessible. How these latter habitats function in the wet season is not known, but given their hydrological condition, it seems likely their fish assemblages would be different from the dry season. Submerged macrophyte beds were under-represented in this study (n = 1), but retained in analysis because they are considered a critical habitat. Normally the LOR supports extensive beds of submerged macrophytes, extending in places ~ 30 m into the channel and to a depth of 2–3 m (A. Storey, pers. obs.). Sampling of these beds in subsequent studies showed they provide important habitat for small and juvenile fish, particularly *Glossamia aprion* (Richardson), *Ammiataba percoides* and *Hypseleotris compressa* (Kreft), as well as supporting large numbers of *Macrobrachium* prawns and atyid shrimps (A. Storey, unpub. data). However, prolonged flooding in the previous wet season (1:20 rainfall event which resulted in extended over-topping of the ORD) had scoured nearly all of the weed beds from the channel, and at the time of this study they had not re-established. Local fishers reported difficulty in obtaining 'bait fish' (small species and juveniles of larger species) during the dry season in the current study which they attributed to the absence of weed beds, suggesting they were important habitat for these fish.

Table 7 Results of multivariate multiple regression of species presence-absence data on environmental variables. %Var. = percentage of variance in species data explained by the environmental variables individually or through stepwise forward-selection; Cum.% = cumulative percentage of variance explained. Refer Table 1 for environmental variable codes.

	Variable	%Var.	F	p	Cum.%
Late dry	***Individually***				
	bkang	24.5	9.419	0.0001	
	depM	21.9	8.112	0.0001	
	cmplx	17.2	6.029	0.0001	
	snag	13.9	4.684	0.0006	
	pebb	9.0	2.864	0.0099	
	Fitted stepwise				
	bkang	2	9.419	0.0001	24.5
	pebb		3.224	0.000	32.3
Late wet	***Individually***				
	cmplx	18.2	6.249	0.0001	
	depM	17.9	6.115	0.0003	
	snag	17.8	6.050	0.0002	
	rootm	16.8	5.634	0.0002	
	subm	16.7	5.600	0.0001	
	pH	11.8	3.760	0.0039	
	vel	10.6	3.419	0.0075	
	cmpct	9.6	3.056	0.0084	
	depV	7.8	2.116	0.0381	
	Fitted stepwise				
	cmplx	18.2	6.249	0.0001	18.2
	subm	8.3	3.067	0.0036	26.6
	depM	7.1	2.796	0.0072	33.7
	rvegco	5.6	2.339	0.0209	39.4

Types of functional habitats

Analysis of habitats at the broadest level showed deep and shallow water habitats to be functionally distinct. But within these two groups, not all habitats consistently separated on the basis of fish assemblages. In the dry season, shallow backwaters, gravel-cobble runs and pools were most distinct, and in the wet season, floodplain habitat, shallow backwaters, emergent and flooded riparian vegetation were most consistently different from all other habitats. Seasonally, there was greater distinction in terms of physical condition between habitats in the late dry season than the late wet, and a greater number of species showed significant habitat preferences in the dry than the wet season. Four functional habitats could be differentiated in the dry season on the basis of their physical attributes and fish assemblages: shallow backwaters, gravel-cobble runs, channel pools and flooded riparian vegetation. In the wet, emergent macrophyte habitat could also be differentiated, but not channel pools. A relatively small number of physical variables could be used to account for a significant proportion of the variation in species assemblages across habitats. The significant differences in community metrics and their positive correlation to water depth and habitat complexity was consistent with the currently accepted hypotheses of fish-habitat interactions that are largely based on Northern Hemisphere observations (e.g. Cowx & Welcomme 1998; Martin-Smith 1998; Robertson & Winemiller 2003). Our results build on previous findings that these hypotheses appear to hold true for Australian rivers (Pusey *et al.* 1993, 2000; Bishop *et al.* 2001; Kennard *et al.* 2006), and here as elsewhere, fish likely respond to combinations of variables in some hierarchical manner (Rabeni & Jacobsen, 1993; Rayner *et al.* 2008; Bouska & Whitledge 2014). Many Northern Hemisphere studies have indicated that water quality variables, such as temperature, to be influential in species distributions and nestedness at a local scale (see Cook *et al.* 2004; Nykänen *et al.* 2004; Smith & Kraft 2005). Few such relationships were recorded in the LOR, probably reflecting the lack of spatial and temporal variation in water quality variables for the habitats assessed.

A seasonally dynamic fish community structure within habitat patches was also to be expected given the variable flow conditions in the LOR. Greater discharge in the late wet season resulted in greater water velocities than in the dry, particularly in pools (mean velocity of 36 cm s^{-1} *cf* 14 cm s^{-1}). Water depths showed a similar response. It was noticeable that catches from pools were reduced in the wet. Whilst higher velocities in the wet may have reduced the fishing efficiency of gill nets in pools, these reduced catches were counter-balanced by increased catches in the relatively sheltered deep backwater and flooded riparian habitats where velocity was lower. The same change in distribution in the LOR has been subsequently recorded across habitats in the late dry season (November 2005) and late wet season (May 2006) when sampling by gill net and electrofisher boat (A. Storey, unpub. data). During the current study, water levels in previously shallow backwaters had risen 2–3 m by the late wet season, connecting these habitats to the main channel via areas of flooded riparian vegetation. Therefore, these 'backwaters' no longer provided shallow (0.5 m deep), standing water habitat for small species/juveniles. Instead, the now deep (2.2 m), low flow areas (8 cm s^{-1}) were colonised by larger-bodied species that normally resided in pools in the main channel. Similarly, broad benches covered with riparian vegetation exposed in the dry were transformed by inundation in the wet season (~ 2 m deep), providing habitat with velocities lower than those of main channel pools and areas of emergent vegetation. It would appear that species and life stages actively moved to remain within their preferred range of ambient conditions. Seasonal and ontogenetic differences for a range of fish species have been demonstrated elsewhere (Scheideggar & Bain 1995; Grossman & Ratajczak 1998; King *et al.* 2003; Nykänen *et al.* 2004), with these studies indicating that optimum conditions typically exist only for relatively narrow zones within habitat patches. During the wet season, vertical segregation is also likely to play a greater role in enabling co-existence of multiple species and life stages in the deepwater habitats, however, this aspect was not directly addressed by the current sampling regime.

Sampling limitations

Sampling methods used in the current study were those readily available and considered most effective to maximise abundance and diversity of fishes in the habitats being surveyed; multipanel gill nets in deeper water and seine netting in shallow water. Multipanel gill nets are effective across a range of habitats, except in shallow water habitats. Whereas seine netting is effective in shallow waters, but not in deep water habitats. It is acknowledged that neither method is ideal as seine netting will likely bias towards large numbers of small bodied, and less mobile species, whilst gill netting will likely bias towards mobile, larger-bodied species. Sampling with the seine net, especially in shallow backwaters was considered very effective, as the whole backwater was seined, and sequential seine hauls through backwaters seldom caught additional taxa after the first haul (A. Storey, unpubl. data). Therefore species richness for backwaters is considered accurate, and the absence of larger-bodied species a good reflection of assemblage composition. Subsequent sampling of fish assemblages of selected deepwater habitats in the Ord using gill nets and boat electrofishing (A Storey & A Berguis, Qld DPI Unpub. dat.), showed gill nets captured approximately 85% of the species taken by electrofishing. Occasional specimens of sedentary species were caught by the electrofisher but not by gill netting, such as sleepycod *Oxyeleotris selheimi*. The boat electrofisher also occasionally caught small-bodied species such as *Glossogobius giuris*, *Melanotaenia australis* and *Craterocephalus stramineus*. However, these latter species tended to be taken when the electrofisher boat moved into shallow areas along the bank, rather than from deep water, pool habitat *per se*. Allowing for these differences, gill netting and boat electrofishing provided very similar assemblage data, suggesting gill nets do represent fish assemblages of the habitats sampled in the LOR. Even so, the inherent problems in comparing catch data from different methods over different spatial scales are well documented (Maunder *et al.* 2006) and are a consideration in the current study.

Species-, age- or size-selectivity of techniques and catchability of species means that individual methods are not always comparable, and this undoubtedly holds true for the current study. Unfortunately there is no single sampling technique that is effective across multiple habitats, particularly in large, spatially complex rivers such as the LOR. If habitat use by fishes is to be compared across multiple habitats, then a combination of techniques is justified if each method provides a true representation of fish assemblages in each habitat. It is considered that methods used in this study meet this objective, but even so, observed trends in the data were interpreted with due consideration of capture method. Comparing species richness across methods, particularly where one method catches greater abundances than another, is prone to error (Gotelli & Colwell 2001), because species richness is known to increase with abundance of specimens captured (Chao *et al.* 2005; Ebner *et al.* 2008). Therefore, direct comparison of species richness of samples with high abundance against those of lower abundance may be misleading. Rarefaction of samples (Gotelli & Colwell 2001) was used to re-estimate species richness and thereby reduce the effect of sampling method on species richness.

Results from this study align with those reported extensively in the literature. Power (1984), Power *et al.* (1985) and Schlosser (1987) all reported habitat segregation, whereby large piscivorous fish forced small fish into shallow refuges. Similarly, Finger (1982), Schlosser (1982a, b), Moyle & Baltz (1985) and Bain *et al.* (1988) all noted that shallow and slow-flowing areas were used by small, young fish of several species, and deep areas were primarily inhabited by larger, older fish. This concordance provides confidence in the efficacy of the methods utilised in this study.

Ecologically relevant water provision

If the biotic integrity of the LOR is to be maintained, then the risk posed by water abstraction should be assessed at the habitat scale, and particularly in the dry season when habitats were most distinct, species preferences the highest, and shallow habitats the most susceptible to change due to reduced water levels (Trayler *et al.* 2002; Storey & Trayler 2006). The current study demonstrates the importance of shallow-water habitats to small-bodied species and juveniles of larger species. Hydrological studies have indicated that even small changes in depth are likely to substantially alter the availability of shallow water habitats in the LOR (Trayler *et al.* 2002; Storey & Trayler 2006), and given the clear preference of small fishes for these habitats, a reduction in lateral habitat will potentially lead to a loss of biodiversity. Relationships between shallow habitats and fish assemblages have been reported previously. Cowx & Welcomme (1998) report shallow, lateral habitats as important for young-of-the-year fish, providing low velocity zones, food resources, protection from deep-bodied piscivores and physical cover, with an increase in area of lateral habitat resulting in increased density of age-0 fish, but a reduction in lateral habitat correlated with elimination of young-of-the-year fish (Cowx & Welcomme 1998). And in an impounded river in southeastern Wyoming, Patton & Hubert (1993) considered that continued loss of shallow backwater and side-channel habitats as a result of reduced flows would lead to loss of species from the system.

Of the 38 species recorded in the current study, autecology has been detailed for at least 20, but is based predominantly on surveys of populations in the Alligator Rivers region, approximately 800 km east of the Ord River system (see Bishop *et al.* 2001), and Queensland (see Pusey *et al.* 2004). It is not known if the biology of these species is the same in the heavily regulated LOR as in their natural habitat, or how species have adapted to the modified flow regime. A number of the species detailed by Bishop *et al.* (2001) and Pusey *et al.* (2004) use densely vegetated, seasonally inundated floodplain habitats for spawning and larval nursery areas. Though spawning is not necessarily restricted to the floodplain, there is increasing evidence from studies of other Australian river systems that floodplains and flooding play an important role in the general ecology of many freshwater fishes (Koehn 2000; Puckridge *et al.* 2000; Schiller & Harris 2001; Balcombe *et al.* 2007). In the LOR however, connectivity with the historic floodplain has been lost as current regulation prevents wet season flows of sufficient magnitude. It seems likely that floodplain-adapted species must now use the flooded margins of the main channel which lies within the historic active channel. However, the lack of locally derived autoecological information of some species and the complete lack of such information for others, needs redress if the LOR is to be managed in an informed manner, and if tropical rivers in Australia in general are to be managed sustainably.

Maintenance of habitat required by all life stages is critical to the survival of a species, and an inadvertent loss of a key habitat(s) could result in a decline in species diversity. The current study only examined a limited suite of habitats on two occasions, and did not consider the broader context of habitat usage. Cowx and Welcomme (1998) noted that fish in rivers depend on undamaged interactive pathways along four dimensions: longitudinal, lateral, vertical and temporal. Such observations have lead researchers to theorise on the "plasticity" of habitat use whereby fish assemblages can behave either as guilds (associated with discrete habitats) or as part of a continuum, with species responding to individual environmental gradients (see Grossman & Ratajczak 1998; Pusey *et al.* 2000; Erős *et al.* 2005). In our analyses, not all variation in fish assemblages could be explained by measured abiotic variables. Pusey *et al.* (2000) obtained similar results from predictive modelling on four rivers in Queensland, Australia. They suggested that this, coupled with high dissimilarity in fish assemblage composition (as is also reported here) reflected the complexity of habitat segregation between species and life history stages. Assessment of the quality and quantity of a specific habitat in an instance in time, although an important means of considering faunal habitat, may be inadequate and misleading if other spatial or temporal habitat requirements are ignored. For example, habitat for adults may be well managed, but if the specific habitat required by larval or juvenile stages is not available (i.e. low velocity, shallow backwaters), then the species may not proliferate. Nor should habitat patch dynamics be viewed as consistent between faunal groups, especially where they operate at different spatial and temporal scales. Functional habitats for fish are unlikely to correspond precisely to those of macroinvertebrates (*cf* Storey & Lynas 2007). Thus for fishes in the LOR, water depth and velocity are more useful for discriminating functional habitats, whereas percentage cover by cobble substrate and emergent/ submerged vegetation were reported as being important for discriminating habitats for macroinvertebrates (Storey & Lynas 2007).

Buffagni *et al.* (2000) considered that it was possible to maintain specific functional habitats to protect endangered or rare species, or to modify channel morphology to increase hydraulic and habitat heterogeneity. Such applications have commenced in the United Kingdom (Kemp *et al.* 1999), and in northern Italy (Buffagni 2000), where flow was related to occurrences of functional habitat, rather than to taxa preferences for water depth and velocity. Overall, these studies support the use of the FHC in river management. However, without detailed knowledge of life history requirements of resident species it may not be possible to predict all implications of flow regulation. Given the presence of 'functional habitats' in the LOR, the application of the FHC seems an appropriate tool for future management of this river.

This study identified deep channel and shallow, marginal habitats as being important to different components of the fish fauna. Hydraulic modelling has indicated that shallow-water habitats in the dry season are most likely to be affected by further abstraction from this already heavily regulated system (Trayler *et al.* 2002). This potentially places the fauna of these habitats at threat. Although the hydrology of the system is already highly modified, it still supports substantial ecological value, a reflection of establishing a permanent water source in a seasonally dry region. This was acknowledged by the Western Australian Environmental Protection Authority who recommended that any environmental flow should maintain the riverine environmental values established since the construction of the ORD (Trayler *et al.* 2002; Storey & Trayler 2006). Although controversial, this pragmatic decision acknowledged the current, modified, yet arguably high values of the system, and that the dams were not going to be removed (see Storey & Trayler 2006). Our inference is that maintenance of the current array of habitats will help support the current values. Environmental flows for the LOR must be designed to protect and maintain the current distribution and area of these key habitat types to maintain their dependent faunas (*sensu* Buffagni *et al.* 2000). The challenge for hydrologists/ fluviomorphologists is to predict how the distribution of these habitats may change under a new flow regime, a generic issue discussed by Tickner *et al.* (2000). The LOR has a predictable and relatively constant dry season flow however wet season flows are more variable, influenced by infrequent but high magnitude tropical cyclones and monsoon depressions. These events, as has been seen in 2000 and 2001, can re-distribute sediment beds, expose snags, and scour submerged macrophyte beds from the channel. This study provides a snap-shot of habitats and their usage in one wet and one dry season. In reality, multiple years of monitoring of functional fish habitats, across years when certain habitats vary in their availability by orders of magnitudes (i.e. submerged macrophyte beds), ultimately will be required to obtain a better understanding of the influence of water availability on the function and structure of the Lower Ord fish assemblages and habitats.

Given the physically distinct nature of the identified functional habitats, a program to monitor their extent over time was developed in 2003 (A. Marshall & A. Storey, unpub. data). The approach uses high resolution (0.25 m), low level (4 000 ft) digital aerial photography of the channel to quantify the area of each functional habitat as identified for fish (this study) and macroinvertebrate assemblages (Storey & Lynas 2007). In late 2006, the recommended approach was applied to three reaches on the LOR, each 5 km in length. It was recommended that monitoring be conducted in the late dry season over three years prior to and three years after a new flow regime is implemented, to test for any changes in key 'functional' habitats. Subsequent to these investigations, the environmental flow regime for the LOR has been designed to maintain functional habitats, and their associated faunas (WRC 2013).

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APPENDIX

Fish species, number caught and size ranges recorded over two consecutive seasons (late dry and late wet) from eight habitats in the LOR. Codes: FL = fork length, i.e. snout to fork of tail or snout to posterior margin of tail for eel-tailed species; LFM = length at first maturity as estimated by Bishop *et al.* (2001) for fishes in the Alligator River catchment of the Northern Territory. Where LFM differed by > 3mm between sexes, size is indicated for both females (F) and males (M).

Family	Species	Common name	FL mm	LFM mm	Numbers caught Late dry	Late wet
Ambassidae	*Ambassis macleayi* (Castelnau,1878)	Macleay's glassfish	14–53	~30	38	606
	Ambassis sp. (undescribed)	Northwest glassfish	27–65		460	3
	Parambassis gulliveri (Castelnau, 1878)	giant glassfish	29–54		33	21
Anguillidae	*Anguilla bicolor bicolor* McClelland, 1844	Indian short-finned eel	310		1	184
Apogonidae	*Glossamia aprion* (Richardson, 1842)	mouth almighty	19–119	~65	7	4
Ariidae	*Neoarius graeffei* (Kner & Steindachner, 1867)	lesser salmon catfish	85–484	~300	197	1
	Neoarius midgleyi (Kailola & Pierce, 1988)	silver cobbler	160–633		57	32
	Sciades leptaspis (Bleeker, 1862)	triangular shield catfish	230–538	~300	11	0
Atherinidae	*Craterocephalus ?stercusmuscarum* (Günther, 1867)	Fly-specked hardyhead	23–38	~28	23	26
Belonidae	*Strongylura krefftii* (Günther, 1866)	freshwater longtom	189–413	290M, 410F	11	4
Carcharhinidae	*Carcharhinus leucas* (Müller & Henle, 1839)	bull shark	554–1200	>2000	6	12
Latidae	*Lates calcarifer* (Bloch, 1790)	barramundi	130–731	700M, 900F	37	42
Clupeidae	*Nematalosa erebi* (Günther, 1868)	bony bream	20–363	130M, 140F	72	318
Dasyatidae	*Himantura dalyensis* Last & Manjaji-Matsumoto 2008	freshwater whipray	600–1250		1	2
Eleotridae	*Hypseleotris compressa* (Krefft, 1864)	empire gudgeon	22–66	37M, 43F	42	3
Elopidae	*Elops hawaiensis* Regan, 1909	giant herring	337–473		1	1
Engraulidae	*Thryssa* sp.		125–128		4	1
Gobiidae	*Glossogobius giuris* (Hamilton, 1822)	flathead goby	47–92	~35	39	15
	Gobiidae sp. B		25		1	0
Hemiramphidae	*Arrhamphus sclerolepis sclerolepis* Günther, 1866	garfish	203		1	0
Leiognathidae	*Leiognathus equulus* (Forsskål, 1755)	ponyfish	37–73		90	4
Megalopidae	*Megalops cyprinoides* (Broussonet, 1782)	ox-eye herring	120–412	>300	12	11
Melanotaeniidae	*Melanotaenia australis* (Castelnau, 1875)	western rainbowfish	21–70	23	137	106
Mugilidae	*Liza alata* (Steindachner, 1892)	diamond mullet	31–470	>350	478	189
	Mugillidae sp.		95		0	1
Plotosidae	*Neosilurus hyrtlii* Steindachner, 1867	Hyrtl's tandan	155–455	135	8	11
	Plotosidae sp. 1		50–97		0	4
	Plotosidae sp. 2		56–69		0	1
Pristidae	*Pristis pristis* (Linnaeus, 1758)	freshwater sawfish	765		0	1
Scatophagidae	*Scatophagus argus* (Linnaeus, 1766)	spotted scat	23-122		0	2
Sciaenidae	*Nibea squamosa* Sasaki, 1992	scaly croaker	384		0	1
Soleidae	*Leptachirus triramus* Randall, 2007	tailed sole	51-59		0	3
Terapontidae	*Amniataba percoides* (Günther, 1864)	barred grunter	19-89	45F, 65M	54	165
	Hephaestus jenkinsi (Whitley, 1945)	Jenkin's grunter	166-345		0	2
	Leiopotherapon unicolor (Günther, 1859)	spangled perch	96-129	74M, 94F	4	3
	Syncomistes butleri Vari, 1978	Butler's grunter	100-273	235	3	17
Tetraodontidae	*Marilyna meraukensis* (de Beaufort, 1955)	Merauke toadfish	61-136		16	4
Toxotidae	*Toxotes chatareus* (Hamilton, 1822)	seven-spot archerfish	24-272	180M, 190F	33	86

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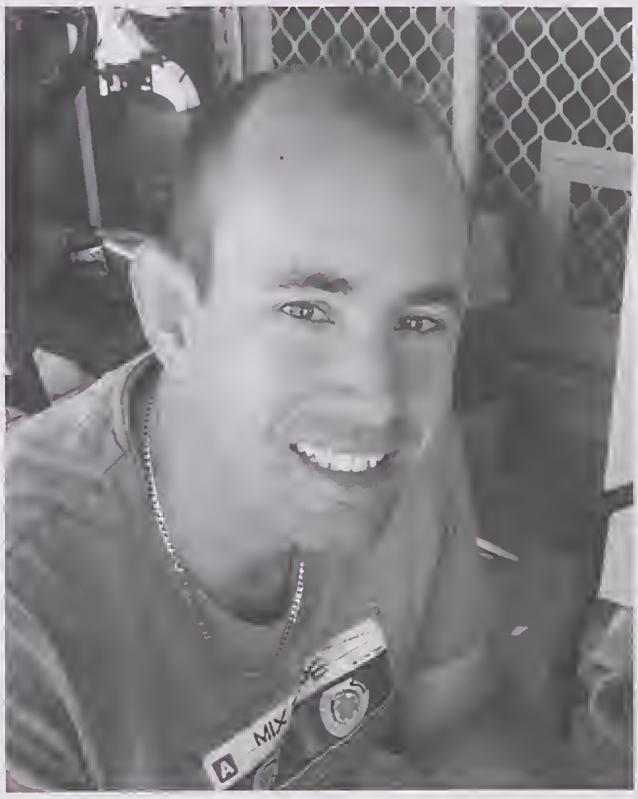
OBITUARY — JONATHAN CHARLES MURPHY 1979–2014

This volume is dedicated to the memory of Jonathan Charles Murphy, who was tragically taken from us in January 2014.

Jon was a talented young biologist who completed a Bachelor of Science with first class Honours in Conservation and Wildlife Biology at Murdoch University, graduating in 2010.

At the time of his death, he was undertaking a Doctor of Philosophy with the Freshwater Fish Group & Fish Health Unit at Murdoch University, studying the molecular phylogenetics of freshwater fishes in south-western Australia.

His exciting discoveries led him to receive an Australian Biological Resources Study Taxonomic Scholarship and the Australian Society for Fish Biology's Barry Jonassen Award in 2011. Jon was passionate about science, about conservation and about the wonderful world of freshwater fishes and will be sorely missed.



Jon Murphy

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